Agricultural Research Institute

PUSA

PROCEEDINGS

LIST

OF THE

COUNCIL AND OFFICERS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.

1924.

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Edward G. Boulenger, *Director of the Aquarium.*

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F. Martin Duncan, F.R.M.S., *Librarian.*

F. W. Bond, *Accountant.*

W. C. Harris, *Chief Clerk.*

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(1924, pp. 697–1176.)

ZOOLOGICAL SOCIETY OF LONDON.

INSTRUCTIONS TO AUTHORS.

Owing to the cost of printing, the Publication Committee beg to draw the attention of Authors submitting papers for publication by the Society to the following Regulations. If the conditions are not observed, papers may have to be returned —

1. MSS. submitted for publication must be written in a clear and legible handwriting, or, preferably, be type-written, and must be in final form for printing. The MSS. should be written on one side of each sheet only, and the pages clearly numbered. All tables of contents, references to plates, or legends to illustrations in the text, etc., must be in their proper places, **with page and plate numbers left blank**; and the position for the text-figures must be indicated. References to literature must be exact, with the page number as well as the volume number and date.

2. Proofs and their Correction.—Two copies of the slip proof, and a page proof for final revision, will be sent to the Author, **but it is important that all serious corrections be made on the slip proof.** Expenses for proof corrections are very heavy, but, if the MSS. comply with Regulation 1, should not exceed 25 per cent. of the printers' charges. If the cost of corrections exceeds 25 per cent., a proportion of the excess will be charged to the Author.

3. Revised proofs must, if possible, be returned within one week from the date of their receipt by the Author.

4. The Author receives 30 copies of reprints free, and, with the sanction of the Publication Committee, may obtain leave to buy extra copies, at the cost price charged by the printers and engravers to the Society. The number of separate copies required must be stated when returning the proof.

5. Illustrations.—Drawings intended to be reproduced as line-block text-figures should be drawn with a good black ink, such as "Process Black" or the best "Indian ink" on white "Bristol board." All lines and dots must be clear and sharp, and no washes or colours used. Wash drawings are not suitable for reproduction as text-figures. All necessary lettering must be clearly, but lightly, indicated in pencil, so that the engravers

may insert sharp, well-drawn letters. Each drawing should be numbered to tally with the text-figure number given in the MSS., and be accompanied by a short, concise, and legible descriptive legend. When making drawings for text-figures, or grouping drawings, it should be borne in mind that, when reduced, the figures must not exceed the dimensions of the printed matter on the page of " Proceedings," viz.:—$3\frac{1}{2} \times 6\frac{1}{2}$ inches. Drawings or photographs intended for reproduction as plates will have to be reduced, when necessary, to fit a space of $4\frac{4}{10} \times 7$ inches.

6. COPYRIGHT.—No use whatever is permitted of the type or illustrations prepared for the Society's Publications other than for the Separate Copies mentioned above, unless the leave of the Committee has been obtained, and recorded on the Minutes. Permission is given only with the consent of the Authors of the papers, if alive, and the source of the text and illustrations shall be stated in the work in which they are used. The use of illustrations from the Society's Publications, if within five years of the date of publication, will be granted only upon the payment of half the cost of their production. All communications made to the Society shall, if accepted for publication, be regarded as the property of the Society, and not returned to the Authors, except for the purpose of comparison with the proof when set up in type.

Note.—The Publication Committee is always ready to give Authors who apply for it, permission to reproduce matter that they have contributed to the Society's " Proceedings " and " Transactions," but the Society has been advised that a formal assignment from Authors is necessary to enable it to protect copyright against third parties.

ZOOLOGICAL SOCIETY OF LONDON.

This Society was founded in 1826 by Sir Stamford Raffles, Mr. J. Sabine, Mr. N. A. Vigors, and other eminent Naturalists, for the advancement of Zoology and Animal Physiology, and for the introduction of new and curious subjects of the Animal Kingdom, and was incorporated by Royal Charter in 1829.

The Society consists of Fellows, Imperial Fellows, Honorary, Foreign, and Corresponding Members, elected according to the By-Laws. It carries out the objects of its foundation by means of its collection of living animals, by its Library, and by its Scientific Publications.

The Office of the Society, Regent's Park, N.W.8, where all communications should be sent, addressed to "The Secretary," is open from Ten till Five, except on Saturdays, when it closes at ONE P.M.

The Library, under the superintendence of Mr. F. Martin Duncan, F.R.M.S., F.R.P.S., F.Z.S., is open daily (except Sunday) from Ten A.M. till Five P.M. ; on Saturdays, Ten A.M. till One P.M.

The Library is closed from Good Friday to Easter Monday, and upon all other Bank Holidays. It is also closed annually for cleaning during the month of September.

The Meetings of the Society for General Business are held in the Meeting Room at the Society's Office on the third Wednesday of the month at 4.30 P.M. except in September and October.

The Meetings for Scientific Business are held in the Meeting Room at the Society's Office fortnightly on Tuesdays, except in July, August, September, and December and January, at half-past Five o'clock P.M.

The Anniversary Meeting is held on the 29th of April, or the nearest convenient day, at Four P.M.

The Society's Gardens are open daily from Nine o'clock until Sunset, or 8 P.M. when sunset is later. Dr. G. M. Vevers is the Superintendent, Mr. D. Seth-Smith, Curator of Mammals and Birds; Mr. Edward G. Boulenger is Director of the Aquarium; Miss Joan B. Procter, F.L.S., is Curator of Reptiles; Miss L. E. Cheesman, F.E.S., is Curator of Insects; Dr. C. F. Sonntag is Anatomist; Dr. H. H. Scott, Pathologist; Prof. R. T. Leiper, F.R.S., with the assistance of a panel of experts, examines and reports on the Parasites; Prof. G. H. Wooldridge, F.R.C.V.S., is Honorary Consulting Veterinary Surgeon; and Dr. R. W. A. Salmond, O.B.E., Honorary Radiologist to the Society. Applications for anatomical or pathological material, or for facilities for work in the Prosectorium should be addressed to the Secretary.

TERMS FOR THE ADMISSION OF FELLOWS.

FELLOWS pay an Admission Fee of £5, and an Annual Contribution of £3, due on the 1st of January, and payable in advance, or a Composition of £45 in lieu thereof; the whole payment, including the Admission Fee, being £50.

No person can be deemed a FELLOW until the Admission Fee and first Annual Subscription of £3 have been paid, or the annual payments have been compounded for.

FELLOWS elected in November and December are not liable for the Subscription for the year in which they are elected.

PRIVILEGES OF FELLOWS.

FELLOWS have Personal Admission to the Gardens upon signing their names in the book at the entrance gate, and may introduce Two Companions daily.

The WIFE or HUSBAND of a FELLOW can exercise these privileges in the absence of the Fellow.

Until further notice, FELLOWS will receive 40 undated Green Cards, available on any Sunday or week-day up to the end of February of the year following the year of issue, and 20 White Cards available on any week-day up to the same date. Twenty of the Green Cards may be exchanged for a book containing two Orders for each Sunday in the year. Twenty White Cards may be exchanged for a book of dated Week-day Orders, each Order available for any day during the week except Sunday. Special children's tickets are no longer issued, but the Green and White Cards are perforated, and each half is valid for a Child under twelve years of age. It is particularly requested that Fellows *will sign every ticket* before it goes out of their possession. Unsigned tickets are not valid.

FELLOWS are not allowed to pass in friends on their written order or on presentation of their visiting cards.

AQUARIUM.—From January 1st, 1925, until further notice, FELLOWS have free personal admission to the Aquarium at all times when it is open. On Sundays, but not on week-days, they may introduce two visitors with them. These privileges are personal and cannot be transferred. For admission to the Aquarium of other friends whom they have admitted to the Gardens by Sunday tickets they may purchase from the Office books of 20 tickets for £1, or a smaller number at the same rate, each ticket admitting one adult or two children on Sundays or week-days. FELLOWS may also purchase a transferable AQUARIUM IVORY TICKET, for £10, valid for the whole duration of the Fellowship and admitting daily, on Sundays or week-days, two persons who have already gained admission to the Gardens.

FELLOWS have the privilege of receiving the Society's ordinary Publications issued during the year upon payment of the additional Subscription of One Guinea. This Subscription is due upon the 1st of January, and must be paid before the day of the Anniversary Meeting, after which the privilege lapses. FELLOWS are likewise entitled to purchase these Publications at 20 per cent. less than the price charged to the public. A further reduction of 20 per cent. is also made upon all purchases of Publications issued prior to 1881, if above the value of Five Pounds.

FELLOWS also have the privilege of subscribing to the Annual Volume of 'The Zoological Record,' which gives a list of the Works and Publications relating to Zoology in each year, for the sum of Two Pounds Ten Shillings. Separate divisions of volumes 39 onwards can also be supplied. Full particulars of these publications can be had on application to the Secretary.

Fellows may obtain a Transferable Ivory Ticket admitting two persons, available throughout the whole period of Fellowship, on payment of Ten Pounds in one sum. A second similar ticket may be obtained on payment of a further sum of Twenty Pounds.

Any Fellow who intends to be absent from the United Kingdom during the space of at least one year, may, upon giving to the Secretary notice in *writing*, have his or her name placed upon the "dormant list," and will then be called upon to pay an annual subscription of £1 only during such absence, or in the event of returning to the United Kingdom before June 30th in any year to pay the balance of the ordinary subscription. After three years a Dormant Fellow must make a further application to be retained on that list.

Any Fellow, having paid all fees due to the Society, is at liberty to withdraw his or her name upon giving notice in *writing* to the Secretary.

Ladies or Gentlemen wishing to become Fellows of the Society are requested to communicate with "The Secretary."

<div align="right">

P. CHALMERS MITCHELL,

Secretary.

</div>

Regent's Park, London. N W. 8.
December, 1924.

MEETINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON

FOR

SCIENTIFIC BUSINESS.

1925.

Tuesday, February	......	3 and 17.
„	March	4 and 17.
„	April	7 and 21.
„	May	5 and 19.
„	June	9.
„	October	20.
„	November	3 and 17.

The Chair will be taken at half-past Five o'clock precisely.

ZOOLOGICAL SOCIETY OF LONDON.

LIST OF PUBLICATIONS.

THE scientific publications of the Zoological Society of London are of two kinds—" Proceedings," published in an octavo form, and " Transactions," in quarto.

According to the present arrangements, the " Proceedings" contain not only notices of all business transacted at the scientific meetings, but also all the papers read at such meetings and recommended to be published in the " Proceedings " by the Committee of Publication. A large number of coloured plates and engravings are issued in the volumes of the " Proceedings," to illustrate the new or otherwise remarkable species of animals described therein. Amongst such illustrations, figures of the new or rare species acquired in a living state for the Society's Gardens are often given.

The " Proceedings " for each year are issued in four parts, paged consecutively, during the months of March, June, September, and December. From January 1901 they have been issued as two half-yearly volumes, indexed separately.

An " Abstract of the Proceedings " is published by the Society on the Tuesday following the date of the Scientific Meeting to which it refers. It is issued along with the " Proceedings," free of extra charge, to all Fellows who subscribe to the Publications, but it may be obtained on the day of publication at the price of Sixpence, or, if desired, sent post free for the sum of Six Shillings per annum, payable in advance.

The " Transactions " contain such of the communications made to the Scientific Meetings of the Society as, on account of the nature of the plates required to illustrate them, are better adapted for publication in the quarto form. They are issued at irregular intervals.

Fellows and Corresponding Members, upon payment of a Subscription of One Guinea *before* the day of the Anniversary Meeting, are entitled to receive the Society's Publications for the year. They are likewise entitled to purchase the Publications of the Society at 20 per cent. less than the price charged to the Public. A further reduction of 20 per cent. is made upon purchases of Publications issued prior to 1881, if they exceed the value of Five Pounds.

Fellows also have the privilege of subscribing to the Zoological Record for a sum of Two Pounds Ten Shillings (which includes cost of delivery), payable on the 1st of July in each year; but this privilege is forfeited unless the subscription be paid *before* the 1st of December following.

The following is a complete list of the publications of the Society already issued.

TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

4to. 20 vols. and Index.

					Price to Fellows.			Price to the Public.		
Vols. I.-IV. (out of print).										
Vol. V., containing 67 Plates .. (1802-66)					5	4	3	6	19	0
„ VI., „ 92 „ .. (1866-69)					11	5	0	15	0	0
„ VII., „ 73 „ .. (1869-72)					10	4	0	13	12	0
„ VIII., „ 82 „ .. (1872-74) ...					9	8	3	12	11	0
„ IX., „ 99 „ .. (1875-77) ...					12	1	6	16	2	0
„ X., „ 95 „ .. (1877-79)					10	0	3	13	7	0
Index, Vols. I.-X. .... (1833-79)					0	7	6	0	10	0
Vol. XI., containing 97 Plates .. (1880-85)					9	12	0	12	16	0
„ XII., „ 65 „ .. (1886-90)					5	8	0	7	4	0
„ XIII., „ 62 „ .. (1891-95)					6	8	3	8	11	0
„ XIV., „ 47 „ .. (1896-98)					5	5	0	7	0	0
„ XV., „ 52 „ .. (1898-1901) ..					5	15	6	7	14	0
„ XVI., „ 38 „ .. (1901-1903) ..					5	8	0	7	4	0
„ XVII., „ 41 „ .. (1903-1906) ..					5	18	6	7	18	0
„ XVIII., „ 43 „ .. (1907-1911) ..					4	1	0	5	8	0
„ XIX., „ 24 „ .. (1909-1910) ..					10	4	0	13	12	0
„ XX., „ 53 „ .. (1912-1915) ..					11	10	3	15	7	0
„ XXI.—Part 1. (7 Plates & 12 Text-figs.)										
(June 1916)					2	5	0	3	0	0

Since 1916 (Vol. XXI. Part I.) publication of the Society's
Transactions has been temporarily suspended, owing to
the high cost of production.

In consequence of a re-arrangement of the stock of the 'Transactions,' the Society is
now able to offer for sale, at the reduced price of £30, sets of Vols. V.-XVI. inclusive.

PROCEEDINGS OF THE COMMITTEE OF SCIENCE AND CORRESPONDENCE OF THE ZOOLOGICAL SOCIETY OF LONDON. 8vo. 2 vols. (Letterpress only).

			Price to Fellows.	Price to the Public.
Part I. 1830-31. 1 vol. 8vo., out of print.				
„ II. 1832. „			4s. 6d.	.... 6s.

PROCEEDINGS OF THE ZOOLOGICAL SOCIETY OF LONDON.

FIRST SERIES.

Parts I.–XV. (1833–1847). 8vo. 15 vols. (Letterpress only.) Price to Fellows : 4s. 6d. each part ; to the Public, 6s.

Index 1830–1847. Price to Fellows : 4s. 6d. ; to the Public, 6s.

Parts I., VII.–IX., XI., XIV., XV., out of print.

SECOND SERIES.

Parts XVI.–XXVIII. (1848–1860). 8vo. 13 vols. (Letterpress only.) Price to Fellows : 4s. 6d. each part ; to the Public, 6s.

Index 1848–1860. Price to Fellows : 4s. 6d. ; to the Public, 6s.

The Parts of this series containing Coloured Plates are out of print.

PROCEEDINGS OF THE SCIENTIFIC MEETINGS OF THE ZOOLOGICAL SOCIETY OF LONDON. 8vo.

	Letterpress only.		With Plates uncoloured.		With Plates coloured.	
	Price to Fellows.	Price to the Public.	Price to Fellows.	Price to the Public.	Price to Fellows.	Price to the Public
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1866 ..	4s. 6d.	.... 6s.†	...... 9s.	.... 12s.†	...... 33s. 9d.	.... 45s
1867	....		...... 9s.	.... 12s.*	...... 33s. 9d.	.... 45s.
1868	....		...... 9s.	.... 12s.	...... 33s. 9d.	.... 45s.
1869	....		...... 9s.	.... 12s.	...... 33s. 9d.	.... 45s.
1870	....		...... 9s.	.... 12s.	...... 33s. 9d.	.... 45s.
Index, 1861–1870	....		4s. 6d.	.... 6s.		
1871	....		...... 9s.	.... 12s.*	...... 33s. 9d.	.... 45s.
1872	....		...... 9s.	.... 12s.*	...... 33s. 9d.	.... 45s.†
1873	....		...... 9s.	.... 12s.	...... 33s. 9d.	.... 45s.
1874	....		...... 9s.	.... 12s.†	...... 36s.	.... 48s.†
1875	....		...... 9s.	.... 12s.	...... 36s.	.... 48s.
1876	....		...... 9s.	.... 12s.	...... 36s.	.... 48s.†
1877	....		...... 9s.	.... 12s.	...... 36s.	.... 48s.
1878	....		...... 9s.	.... 12s.	...... 36s.	.... 48s.
1879	....		...... 9s.	.... 12s.	...... 36s.	.... 48s.
1880	....		...... 9s.	.... 12s.	...... 36s.	.... 48s.
Index, 1871–1880	....		4s. 6d.	.... 6s.		
1881–1890. Ten volumes	.... Each		....		36s.	.... 48s.
Index, 1881–1890	....		4s. 6d.	.... 6s.		
1891–1900. Ten volumes	.... Each		....		36s.	.... 48s.
Index, 1891–1900	....		4s. 6d.	.... 6s.		

* No perfect copies in stock. † Out of print.

PROCEEDINGS of the GENERAL MEETINGS for SCIENTIFIC BUSINESS of the ZOOLOGICAL SOCIETY OF LONDON

(*continued*).

	Price to Fellows.	Price to the Public.
1901–1910. Twenty volumes .... Each 18s.		24s.
Index, 1901–1910 .... 4s. 6d.		6s.
Index, 1911–1920 .... 8s.		10s.
1911–1916. Twelve volumes .... 18s.		24s.
1917, vol. I.................................... 18s.		24s.
„ „ II. .... 9s.		12s.
1918. Two volumes .... 9s.		12s.
1919. Two volumes .... 15s.		20s.
1920, vol. I. .... 15s.		20s.
„ „ II. .... 18s.		24s.
1921. Two volumes .... 18s.		24s.
1922. Two volumes .... 18s.		24s.
1923. Two volumes .... 18s.		24s.
1924, vol. I. .... 18s.		24s.

LISTS OF THE ANIMALS IN THE SOCIETY'S GARDENS.

List of the Vertebrated Animals now or lately Living in the Gardens of the Zoological Society of London. (Eighth Edition.) 8vo. 1883.   Cloth, 4s. 6d.

List of the Vertebrated Animals now or lately Living in the Gardens of the Zoological Society of London. (Ninth Edition.) 8vo. 1896.   Cloth, 6s.

CATALOGUE OF THE LIBRARY of the Zoological Society of London (Fifth Edition.) 8vo. 1902.   Cloth, 6s.

THE OFFICIAL ILLUSTRATED GARDEN GUIDE—22nd Edition (Revised)—with (1) a Railway and Street Map; (2) a Plan of the Grounds; (3) a short description of some of the principal animals in the Collection, with 52 Photographic Illustrations and Index. Price 1s. in Stiff Paper Cover, postage 2d.

ZOOLOGICAL RECORD.—Vol. 59, containing literature relating chiefly to the year 1922, will be published in July 1924, price £3. Vol. 60, for the year 1923, is being prepared as usual, price £3, or subscription, if paid in advance, £2 10s. 0d.

P. CHALMERS MITCHELL,
Secretary.

Regent's Park, London, N.W. 8.
December, 1924.

These publications may be obtained at the SOCIETY'S OFFICE *or through any bookseller.*

PROCEEDINGS

GENERAL MEETINGS FOR SCIENTIFIC BUSINESS

ZOOLOGICAL SOCIETY OF LONDON

PAPERS.

28. Some External Characters of *Orycteropus afer* *.
By R. I. POCOCK, F.R.S., F.Z.S.

(Text-figures 1–5.)

CONTENTS.

The Head and its Organs.

The general form of *Orycteropus*, its long narrow head, large rabbit-like ears, short neck, heavily-built body, arched back, muscular tapering tail, powerful and essentially digitigrade limbs, are well known; but many of its external characters do not appear to have been described in detail.

* Based upon South African and Abyssinian examples examined in the Society's Prosectorium and at the Natural History Museum.

The *head*, which, except in the region of the mouth, is covered with short hairs, is gradually narrowed distally down to the muzzle, which is expanded and overlaps the lower jaw to a considerable extent. The gape of the mouth is comparatively short ; and the eye, set about half-way between the angle of the mouth and the base of the ear, is tolerably large.

The *facial vibrissæ*, except the mystacials which are few in number and evidently from their shortness of no great importance, are well developed, long, and tolerably numerous. The interramal tuft is represented by about four long bristles rising from a wart-like eminence set as far back as the eye. There is a single well-developed genal tuft on each side, also rising from a wart-like eminence, which is set high up beneath and a little

Text-figure 1.
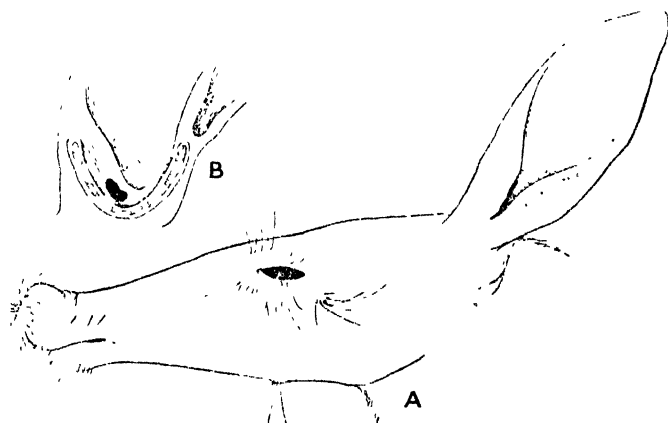
A. Side view of the head to show the general shape, the ear, snout, and facial vibrissæ.

B. Base of the cavity of the ear cut open to show the orifice, the downward extension of the anterior ridge and the lower portion of the pouch on the posterior flap partially contracted by the overfolding of its edges.

behind the posterior angle of the eye. In front of it there is a longish line of subocular bristles; and above the anterior angle of the eye may be seen a tuft of superciliaries in addition to some long lashes on the upper lid. Protection of the eye is presumably the function of the vibrissæ arranged round that organ. The chin is provided with many slender submental bristles.

The *snout*, composed of the confluent upper lip and nose, is peculiar, and consists of a muscular swelling covered with loose flexible skin. It is capable of a considerable movement, especially in a vertical plane, and the skin of its upper side is thrown into folds when it is elevated. It is covered with hair except between

the nostrils, where there is an oblong area of naked skin, longer from above downwards than from side to side. This is the last remnant of the naked rhinarium encircling the nostrils in many mammals. The truncated tip of the snout slopes obliquely upwards and backwards, so that the nostrils are invisible from the inferior aspect, but visible from above. The nostrils are nearly vertical slits, bordering laterally the naked internarial area of skin, and are capable of being expanded and tightly closed. They are provided with long hairs forming a fringe

Text-figure 2.
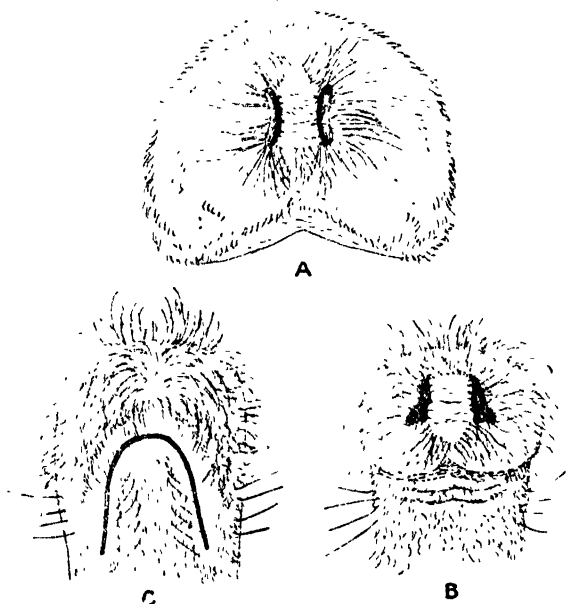
A. Front view of snout showing the naked area of skin between the contracted nostril and the fringes of hair round them.
B. Upper view of the same on a smaller scale with the nostrils more expanded.
C. Lower view of muzzle showing the mouth and the hairy upper lip projecting beyond it.

arising from within the outer edge. There is another fringe above which passes from within the upper inner angle of the nostril upwards and inwards towards the middle line of the snout; and an inferior fringe or tuft somewhat similarly passes from the lower edge of the nostril to the middle line beneath the naked internarial area. These fringes help to block the nostrils when closed by contraction, and their function no doubt is the exclusion of the dust and *débris* arising from the breaking open of termite mounds. The external fringe shows as a prominent

46*

tuft in profile view even when the nostrils are closed. In a
South African example of *O. afer* there were some additional
longer hairs on the underside of the muzzle, which I did not
observe in an Abyssinian specimen usually regarded as belonging
to a second species, *O. æthiopicus*. The skin of the edges of the
upper and lower lips is naked.

The structure of the cavity of the mouth calls for no special
comment. Except for the elasticity of the tongue and the enlarge-
ment of the salivary glands it presents none of the peculiarities
of the mouth of the South American Ant-eaters. The tongue in
a fresh specimen can be stretched to at least double its length
when at rest in the mouth; when contracted it exactly fits the
space between the two mandibular bones, and neither in its
retractor muscles nor in its macroscopic structure could I find
any peculiarity to distinguish it from a normal mammalian
tongue. The palate, too, is ridged, as it is in most mammals.

The long *ears*, narrowed and tubular at the base and attenuated
at the apex, are as movable apparently as the similarly-shaped
ears in rabbits, antelopes, and horses. They are not, however,
strengthened by thickened ridges running from the base towards
the apex, but are kept erect mainly by the stiffness of the
inflected margins of the lower half of the pinna. Just above the
cup-shaped basal portion these edges are separated by a narrow
cleft, expanding distally, and this cleft is capable of expansion
by the contraction of the posterior inflected flap, the anterior
and posterior edges of which can be brought close together, a
deep groove being formed between them *. The structure of the
cavity of the ear is extremely simple. The auditory orifice lies at
the bottom of it, and the only ridge it possesses is the downward
extension of the edge of the anterior flap, which ceases just
above and behind the orifice.

The Feet.

The feet are unlike those of other Ant-eaters in the arrange-
ment of the digits and the suppression of all trace of the plantar
pad. The *fore foot* is tetradactyle, all external trace of the
pollex or first digit having disappeared. The second and third
digits are very nearly equal in length, the latter only slightly
exceeding the former. Although united by webbing extending
to the proximal margins of the digital pads they are tolerably
widely separable; and each carries a powerful claw which
apparently varies in length and sharpness in accordance with
use. The breadth of these claws, if quite short, would entitle

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* In two photographs of a South African and an Abyssinian Aard-vark taken in
the Zoological Gardens by Mr. F. W. Bond, the ears of the former are considerably
narrower in their basal portion than are those of the latter. This difference,
however, is, I think, due to the contraction of the tube of the ear in the one case
and its expansion in the other; and this assumption is borne out by the photograph,
published by Haagner ('South African Mammals,' p. 238), of a South African
specimen with the ears as wide as in the Abyssinian example.

them to be described as "nails" or "hoofs." The fourth digit, although considerably shorter than the third, the distal end of its pad only overlapping to a small extent the proximal end of

Text-figure 3.

A. Fore foot of *O. afer afer* from the outer side.

B. The same of *O. a. æthiopicus* from below, on a larger scale, with the digits spread and the fringes raised.

C. The same of *O. a. afer*, on the same scale as A, with the digits closed and the fringes folded over the sole and the underside of the digits.

the pad of the third, is similar to it in form. It is webbed on its inner side down to its digital pad, but this web is narrower than the web between the second and third digits and does not

reach the proximal end of the pad of the third. The fifth digit is much the shortest of the four, the distal end of its smaller pad falling a long way short of the proximal end of that of the fourth. It is narrowly webbed to the fourth down to its digital pad; but this web does not extend any appreciable distance along the outer side of the fourth. The claw of the fifth is relatively longer than that of the fourth, as the claw of the latter is relatively longer than that of the third or second. Hence shortness of digits in this fossorial foot is compensated by length of claws.

The underside of the digits and of the sole of the foot is covered with soft, naked skin back to the carpus, there being at most a few short hairs near the longer hairs clothing the posterior surface of the wrist. Thus the normal mammalian plantar and carpal pads are entirely wanting; and, when the Aard-vark is walking or standing, only the digital pads and claws rest on the ground, the foot being essentially digitigrade, the greater part of the weight of the forequarters being carried by the second and third digits. But the digital pads vary in degree of development. In an Abyssinian specimen they were large, nearly elliptical, and quite clearly defined by their dark colour and hardness; but in an example from the Cape the skin of the tips of the digits was merely harder and thicker than elsewhere; there was no differentiation of the pads by colour, and proximally they fused imperceptibly with the rest of the skin of the digits.

On the inner side of the foot there is a fringe of long hairs extending from the wrist to the pad of the second digit, and a similar fringe runs along the outer side from the wrist to the pad of the fifth digit. The edges of the remaining digits are also fringed. It seems probable that the function of these fringes is to sweep away the dust and finer rubbish resulting from the demolition of the termite mounds; but, when the fore foot is at rest the fringes curve downwards and inwards so as to underlie and almost to cover the sole and lower sides of the digits.

Except for the presence of the hallux, or first digit, which is a little larger and set a little lower than the fifth, the digits of the *hind foot* in their arrangement, proportions, and webbing are very similar to those of the fore foot. The digital region of the foot generally, with its soft naked skin, digital fringes, and absence of plantar pad, hardly differs from that of the fore foot except that the claws are much shorter and the marginal fringes on the first and fifth digits not so well developed. On the metatarsal area, slightly out of the middle line towards the inner edge, there is a single nearly elliptical pad a little distance above the plantar area. On the plantar side of this there are a few short hairs; but laterally and behind it the metatarsal area is clothed with long hairs directed towards the middle line and upwards, the tip of the calcaneum being naked and padded.

The hind foot is as completely digitigrade as the fore foot, the-

weight of the hindquarters, when the Aard-vark is standing or walking, being supported upon the digital pads and claws of the second, third, and fourth digits, the second and third being the

Text-figure 4.

A. Hind foot of *O. afer æthiopicus* from below, showing the metatarsal pad the naked callous heel, and the digits and fringes spread.

B. The same of *O. a. afer*, on a small scale, from the inner side.

C. The same from the outer side.

most important. The explanation of the retention of a single metatarsal pad and of the development of a pad on the calcaneum

is to be found, no doubt, in the animal's habit of squatting on the entire sole of the foot, with the tail acting as an additional prop, when it is employed in the demolition of a termite mound with its fore feet. For the rest, the hind feet are used for kicking back the loosened soil during the construction of a burrow, and for this purpose the claws and fringes of hairs on the digits are no doubt useful.

I may add that the feet of the Aard-vark, no less than its snout, mouth, and ears, are entirely different from those of *Manis* and of the South American Ant-eaters, *Myrmecophaga*, *Tamandua*, and *Cyclopes*. In these the hind feet are plantigrade, naked back to the heel, and furnished with four or five short, subequal digits set in a transverse line and armed with sharp, compressed claws. The claws of the fore feet are also sharp and compressed, and the outer side of the foot is planted on the ground during progression, with the claws, of which that of the third digit is much the largest, folded inwards and backwards.

Text-figure 5.
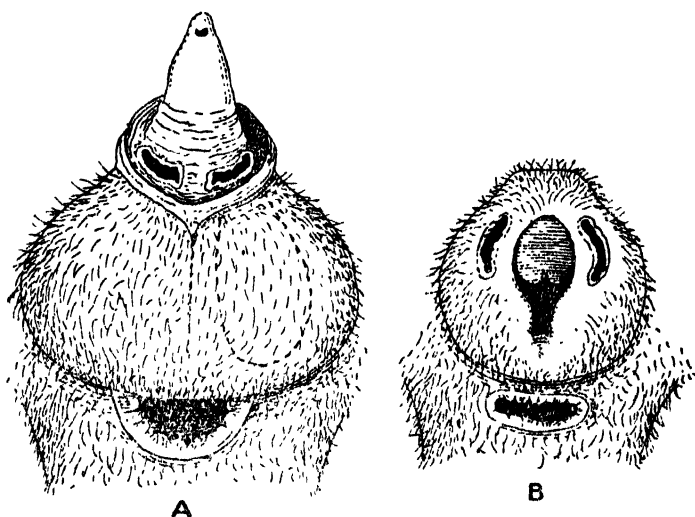
A. Anus and genital eminence of male *O. afer æthiopicus*, showing the penis, 'the orifices of the glandular sacs encircled by ridge of integument forming a sphincter, the outline of one of the imbedded glands indicated by a dotted line.

B. The same of the female, showing the orifices of the glands and the genital orifice with the large heart-shaped clitoris.

The Genital Eminence and its Glands.

In 1916 (Proc. Zool. Soc. pp. 742–744) I described a pair of scent glands on the genital eminence of the male and female of

the South African Aard-vark. The orifices are long slits opening
in the female on each side of the vulva and in the male just
behind the prepuce. The sacs of the glands were described as
short and wide and filled with a yellow secretion smelling like
that of the anal glands of a Polecat (*Mustela putorius*). In a
male of an Abyssinian specimen similar glands exist and the
secretion has the same smell; but, judging from my description
published in 1916, they differ in having the orifices encircled by
a ridge of integument which also encircles the penis and folds
over it when retracted. Thus the orifices of these glands and
the penis can only be seen when this sphincter-like rim of
integument is expanded. The sacs of the glands are also deeper
apparently than they were in the male South African Aard-vark.
These differences require verification on fresh material.

The penis itself is short and soft and shaped like a truncated
cone, the apex being narrowed and carrying the orifice on its
underside.

In the female the glandular sacs are situated, as in the South
African Aard-vark, on each side of the vulva, but apparently a
little more anteriorly. The genital orifice is a long cleft behind
the centre of the genital eminence and preceded by a large
cordate posteriorly bilobed plate, the clitoris. This is capable of
being deflected so that the lobate portion lies anteriorly.

Conclusions.

The external characters of *Orycteropus* throw no light upon
the affinities of the genus.

1. The soft, hairy, muscular, mobile snout, with its terminal
valvular nostrils, is unlike that of any known Mammal. It is,
however, perhaps worth bearing in mind in this connection the
development of a peculiar snout in early Proboscideans. In the
Pholidota and Edentata the snout with its rhinarium is quite
unlike that of *Orycteropus* and more normal in structure.

2. In the Pholidota and Edentate Ant-eaters the genal and
interramal tufts of facial vibrissæ are suppressed, and the
mystacial and submental vibrissæ are so short as to be presumably
functionless. The only members of the Edentata to which
Orycteropus shows resemblance in retaining the genal and
facial vibrissæ are the Armadillos of the genus *Dasypus* and its
allies. This likeness, however, is merely due to the retention of
a primitive character, and as such cannot be regarded as evidence
of affinity.

3. The ear superficially resembles that of many Artiodactyle
Ungulates, but is probably in its simple structure more like
that of the Leporidæ than of any other Mammals. It is
entirely unlike the ear in the Pholidota and the Edentata.

4. The fore and hind paws are entirely unlike those of the
Pholidota despite the general similarity in habits between
Orycteropus and the large terrestrial Pangolins of Africa. They

are also quite unlike the feet of the Edentate Ant-eaters
(*Myrmecophaga* and *Tamandua*). But in the disposition of the
digits and the absence of the plantar pad they certainly show
some likeness to the feet of the Armadillos (*Dasypus*), making
allowance for the retention of the first digit in the latter
animal.

5. The genital eminence with its paired glandular pouches is
unlike the ano-genital eminence of the Pholidota, which owes its
swollen condition mainly to the presence of two enlarged anal
glands. The Edentates have nothing similar to it in any way;
and the penis of the Armadillos is totally different from that of
Orycteropus.

29. The External Characters of the Pangolins (Manidæ).
By R. I. POCOCK, F.R.S.

(Text-figures 6–13.)

CONTENTS.

Introduction.

Pangolins are seldom imported alive to Europe. During the time I was Superintendent of the Zoological Society's Gardens only one example, a specimen of *Manis tricuspis*, was exhibited. Of the external characters of this animal I made sketches and notes immediately after its death. Otherwise I have seen no fresh material. But in the Natural History Museum, in addition to a large number of dried skins and mounted specimens, there are examples preserved in alcohol of *M. tricuspis*, *M. tetradactyla* (=*longicaudata*), and immature individuals of *M. pentadactyla* =*aurita*), and *M. javanica*. Through the courtesy of Mr. R. H. Burne I have also had the opportunity of examining the material, including anatomical preparations, in the Museum of the Royal College of Surgeons. This paper is based upon an examination of this material; but I paid no special attention to the shape, number, and disposition of the scales on the body and tail, since these have been already described in systematic papers.

Although Gray [*] and Fitzinger [†] divided the Pangolins into several genera, which will be referred to later, other monographers of the group, like Jentink [‡] and Matschie [§], assigned all the species to the single genus *Manis*: and their example has been followed, I believe, by all systematic and faunistic writers. This course I propose to adopt in the first part of this paper, leaving to the final part my conclusions respecting the generic subdivisions justified, in my opinion, by the facts established.

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[*] Proc. Zool. Soc. 1865, pp. 363–371; also Cat. Edentate Mamm. 1869.
[†] SB. Akad. Wien, lxv. pp. 9–83 (1872).
[‡] Notes Leyden Mus. 1882, p. 206.
[§] SB. Ges. nat. Fr. Berlin, 1894, pp. 1–11.

The Head and its Sense-Organs.

The *head* is short and conical, tapering to the snout, which is bluntly truncated. The scales extend nearly to the ears, but leave a deeper area above the eyes and usually fail to reach the rhinarium by a considerable distance, as in *M. tricuspis*, but sometimes, as in *M. javanica*, extend almost to it, although in that case they are small and weakly cornified.

Text-figure 6.
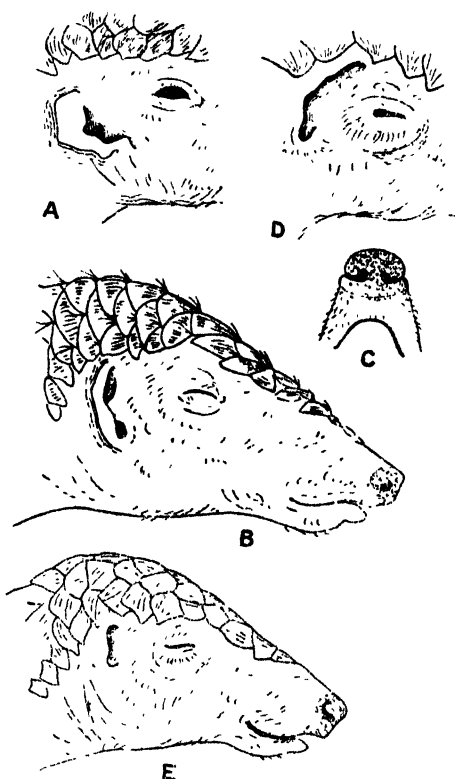
A. Part of the head and ear of young *Manis pentadactyla* from Nepal.

B. Head of young *Manis javanica*.

C. Rhinarium of the same.

D. Part of the head and ear of adult *Manis tricuspis*.

E. Head of newly-born young of the same.

The *eyes* are comparatively small except in *M. tricuspis*, and probably *M. longicaudata*, where they are relatively considerably larger.

The *facial vibrissæ*, as in the American Ant-eaters, are reduced to a few short fine hairs on the lips and round the eyes, the supraorbital, genal, and interramal tufts being aborted.

The *rhinarium* is tolerably well-defined, naked, moist, and areolated. It is without median groove, and the nostrils are narrowly separated in the middle line. They are well developed and normal, being expanded at their antero internal ends and posteriorly form a narrower curved slit.

The *ears* vary considerably in size, but are always comparatively small. They are largest in *M. pentadactyla* (=*auritus*), where each consists of a well-developed flap standing away from the head. The upper edge does not rise above its point of attachment in front. It forms an abrupt angle with the posterior border, which inferiorly is angled and turns forward running into a slightly sinuous inferior border. The shallow cavity of the ear is defined below and behind by a sinuous ridge parallel in a general way to the external edge. In front it forms a small, possibly "tragal" thickening, and behind this there is a wide shallow angular notch. Above and a little behind the notch is the conspicuously exposed orifice.

In *M. javanica* the postero-inferior rim of the pinna seen in *M. pentadactyla* is reduced to a thickened subvertical ridge of integument with a lightly convex, slightly sinuous posterior edge, and a correspondingly concave, more strongly sinuous anterior edge, with a narrow notch below, within which lies the almost concealed orifice. The ear of *M. crassicaudata* is apparently similar to that of *M. javanica*.

In *M. tricuspis* the thickened rim seen in *M. javanica* and *crassicaudata* has entirely disappeared, the posterior border of the slit of the ear which contains the orifice in its lower portion being flush with the skin of the head behind it. In the remaining African species the pinna is said to be similarly absent. No trace of it is detectable on dried skins.

The Fore Foot.

The fore foot has five digits, of which the 3rd is always the largest, and the 2nd and 4th larger than the 1st and 5th, the 2nd, 3rd, and 4th carrying the falcate fossorial claws.

In a newly born young, preserved in alcohol, of *M. pentadactyla* Linn., the arrangement of the digits is nearly symmetrical. They are tolerably evenly spaced. The 1st and 5th are small and sub equal, and are set almost on the same level on the inner and outer sides of the foot respectively, the 1st being only slightly in advance of the 5th. The 2nd and 4th are much larger, and approximately equal in size, and are armed with long pointed, slightly curved claws. The 3rd, in the centre of the foot, is considerably longer and strongr than the 2nd or 4th. The upper surface of the foot is covered with scales down to the base of the claws. The lower surface is quite naked and is covered for the

most part with smooth wrinkled skin, but towards the outer and
inner sides of the sole, behind the 5th and 1st digits respectively,
there is an ill-defined granular pad, the pad on the outer side
behind the 5th digit being set a little farther back than the one
on the inner side behind the pollex.

In the young of *M. javanica* the fore foot agrees in the scaling
of its upper side and in the relative lengths and disposition of its
digits with that of *M. pentadactyla*; but the claws of the 2nd,
3rd, and 4th are more curved and relatively much shorter, and
the sole of the foot is granularly corrugated all over and carries a

Text-figure 7.
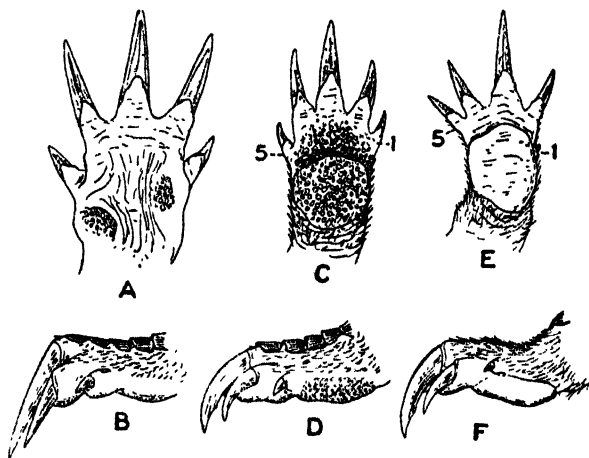
A. Right fore foot of young *Manis pentadactyla* from below.
B. The same from the inner side.
C. Right fore foot of *M. javanica* from below.
D. The same from the inner side.
E. Right fore foot of *M. tricuspis* from below.
F. The same from the inner side.

1 and 5 first and fifth digits.

(Drawn from specimens preserved in spirit.)

single large pad, as wide as the foot, which represents the plantar
or carpal pad, or both combined, of the normal mammalian foot.

Of the third Asiatic species, *M. crassicaudata*, of peninsular
India and Ceylon, I have seen only dried skins, in which the soles
of the fore feet are too shrivelled for accurate interpretation of
the pads; but the digits appear to be quite like those of *M. pen-
tadactyla* and *M. javanica*, although the claws are long as in the
former, being, as in that species, much longer than those of the
hind feet.

Of the two big terrestrial African species, *M. gigantea* and

M. temminckii, I have also seen only dried skins ; but in these I can detect no structural points suggesting any difference of moment from the feet of the three Asiatic species.

But in the two small arboreal African species, *M. longicaudata* and *M. tricuspis*, the fore feet present well-marked differences from those of the other forms of the genus. In the first place, as other observers have noticed, the upper side of the foot is hairy and not scaly. But there are also distinct differences in the digits. The 1st or pollex is minute and represented by little more than a small functionless claw behind the base of the 2nd. The arrangement and relative lengths of the 2nd, 3rd, and 4th are as in the other species, with the claws strongly curved and sharp. But the 5th digit is considerably larger than the 1st, is set far in advance of it and rises from the base of the 4th, to which it is tolerably closely united, more closely than the 2nd is to the 3rd, in a manner indeed suggesting incipient syndactylism. The sole of the foot is quite smooth and carries a well-developed pad similar to that of *M. javanica*, but better defined.

The Hind Foot.

The relative length and disposition of the digits of the hind foot of *M. pentadactyla* and *M. javanica* are nearly the same as in the fore foot in the sense that the 2nd, 3rd, and 4th are the largest and the 1st and 5th the smallest of the five. But in the two young examples of these species examined there are some noticeable differences in their feet. In *M. pentadactyla* the sole is longer and narrowed towards the heel, which is covered with naked wrinkled skin. The anterior part is padded and granular and extends forwards between the 1st and 5th digits, encroaching upon the underside of the 2nd, 3rd, and 4th, up to the level of their fusion, and the 3rd is only a little longer than the 2nd or 4th, the claws and digits being much shorter than in the fore foot.

In *M. javanica*, on the contrary, the pad which, like the area in front of it, is granularly roughened, does not extend forwards between the 1st and 5th digits, but leaves the lower sides of digits 2 to 5 uncovered for some distance behind their point of union. It is quite sharply defined from the scaly skin of the tarsus behind, its posterior third being narrowed, and in front its anterior edge is also more sharply defined than in *M. pentadactyla*, and the 3rd digit is larger as compared with the 2nd and 4th than in that species.

On dried skins of adult and young examples of these two species the most noticeable difference in the hind foot lies in the claws, which are longer, sharper, and more curved in *javanica* than in *pentadactyla*. As others have observed, they are nearly as long in *javanica* as those of the fore foot and are no doubt scansorial in function. In *pentadactyla* they are sometimes tolerably sharp and long, at other times blunt and short, owing

to wear. In one example of this species from Amoy the pad behind the base of the digits is subdivided by radiating grooves into five distinct areas, four of which, forming the curved distal edge of the pad, suggest the four combined lobes of the plantar pad characteristic of many mammals; but considering the dried condition of the specimen it would be unwise to assume that homology.

In dried skins of the common Indian and Ceylonese species, *M. crassicaudata*, the hind foot differs very markedly from that

Text-figure 8.
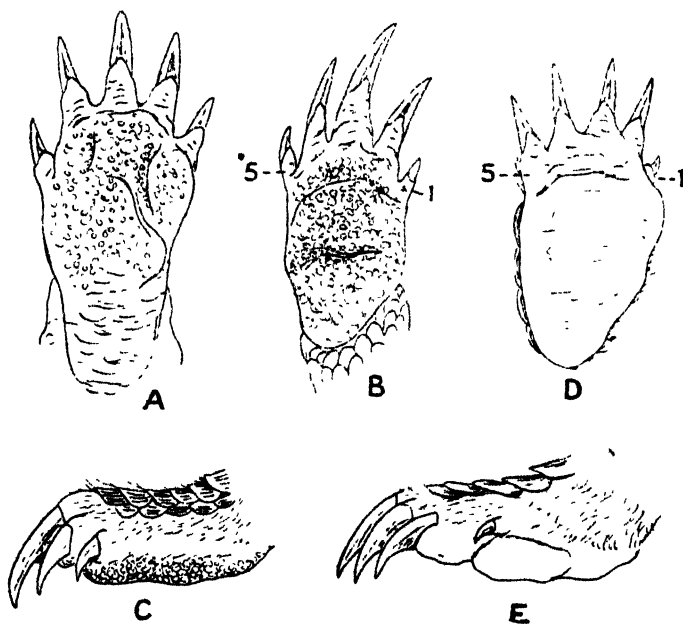
A. Right hind foot of young *Manis pentadactyla* from below.
B. The same of young *M. javanica*.
C. The same from below.
D. Right hind foot of *M. tricuspis* from below.
E. The same from the inner side.

1 and 5 first and fifth digits.

(Drawn from specimens preserved in spirit.)

of *M. javanica*, less so from that of *M. pentadactyla*, which is almost intermediate. It is compact and short and stumpy, the coarsely granular pad extending up to the base of the claws, which are quite short, blunt, slightly curved and depressed over the anterior edge of the pad. Although this foot, judging from its shape, seems designed for walking on the ground, we have the testimony of Sir Emerson Tennant to prove that this Manis is able to climb.

Judging from dried skins and mounted specimens, the hind feet of the large African terrestrial species, *M. gigantea* and *M. temminckii*, are short and stumpy and covered with a continuous pad up to the tips of the short, curved, blunted claws which rest on its anterior extremity, scarcely or not reaching the ground. The claws form an evenly curved line, and there is no

Text-figure 9.
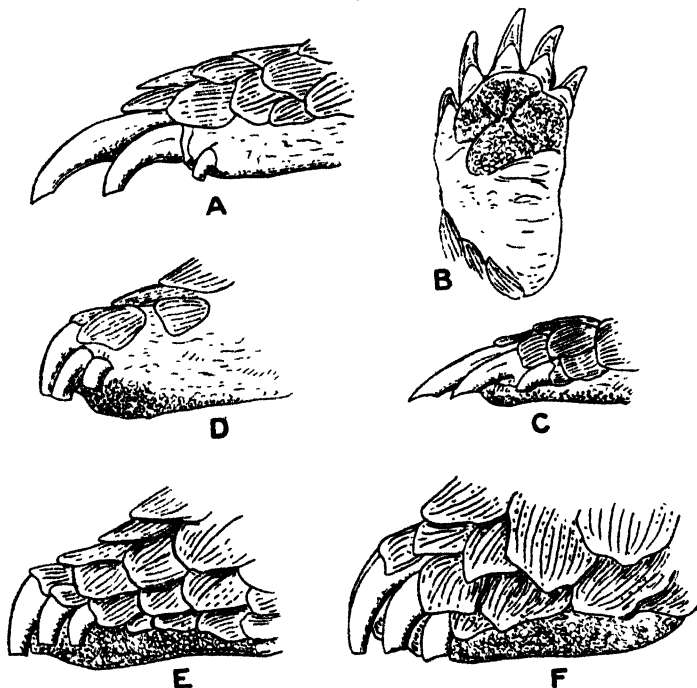
A. Right hind foot of adult *Manis javanica* from the inner side.
B. Right hind foot of adult *M. pentadactyla* from Amoy, from below, showing lobate pad.
C. The same from the outer side.
D. Right hind foot of adult *M. crassicaudata* from inner side.
E. Left hind foot of the same from outer side.
F. Left hind foot of adult *M. gigantea* from the outer side.
(Drawn from dried skins.)

indication of division between the distal ends of the digits. The hind feet of these two species do not appear to differ in any characters of moment from those of the common Indian species, *M. crassicaudata*, and it may be noted that this type of foot seems to be correlated with a rather short but powerful tail.

In *M. longicaudata* and *tricuspis*, the African arboreal species,

the feet are more like those of *M. javanica*, but, as in the case of the fore feet, differ from those of all other Pangolins in the reduction of the hallux, or 1st digit, to an excrescence bearing a very small claw and set behind the base of the 2nd and a long way behind the 5th. The 5th, moreover, is as large as the 4th, 3rd, and 2nd, the four being approximately equal, nearly on a level, and having subequal, sharp, curved claws. The whole of the underside of the foot is smooth and carries a large flat pad which extends from the level of the 1st digit to the heel and has a conspicuous bulge on its inner side behind the hallux.

The Tail.

The tail is always well developed and powerful, and approximately as wide at the base as the anal region; but its well-known variation in length and breadth relatively to the body is very considerable, the extremes being met with in the two African species, *M. longicaudata* and *M. temminckii*. The number and shape of the scales have been described by various authors, and

Text-figure 10.
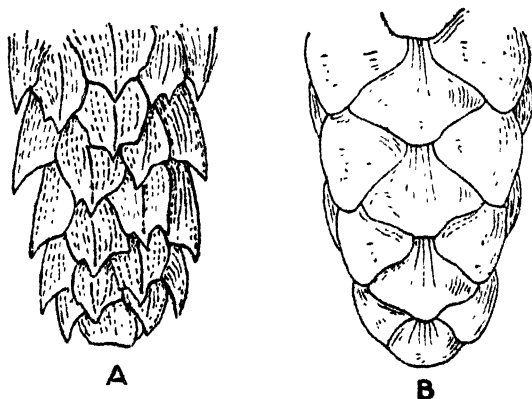
A. Upper side of end of tail of *Manis tricuspis*, showing the irregular arrangement of the scales.

B. The same of *M. pentadactyla*, showing the regular arrangement of the scales and bristles projecting beneath the median series.

many systematists have recorded the puzzling difference between the four African species and the three Asiatic species in the arrangement of the scales at the tip of the dorsal side of the tail. In the Asiatic species the arrangement is almost always * symmetrical, the median series of scales being continued uninterruptedly to the tip, whereas in the African species the median row is represented by two rows of asymmetrically disposed scales at the distal extremity of the organ.

* Shown to be variable in *M. crassicaudata* by Anthony (Bull. Mus. Paris, xxv. pp. 17, 18, 1919).

The presence or absence of a naked cutaneous pad at the tip of the tail beneath has also been described. It attains its highest development in the two West African arboreal species, *M. longicaudata* and *M. tricuspis*, where it is comparatively wide and truncated and indistinctly bilobed at its distal end. Proximally to it there is a median area of skin left naked by the absence of two median and two lateral scales. In the newly-born

Text-figure 11.
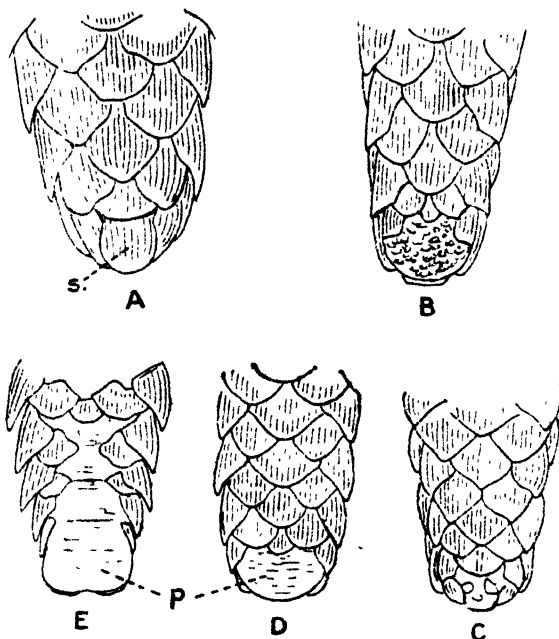
A. Lower side of end of tail of adult *Manis crassicaudata*, showing the terminal scale (*s*).
B. The same of adult *M. pentadactyla* from Upper Burma, showing the granular terminal pad.
C. The same of a young specimen from Nepal.
D. The same of *M. javanica*, showing the naked terminal pad (*p*).
E. The same of *M. tricuspis*, showing the naked terminal pad (*p*) and the naked skin above it.

(A and B from dried skins: C, D, E from spirit specimens.)

young example of *M. javanica* the pad is also present, but it is shorter and relatively narrower than in the two species just described and has an evenly convex edge. There is also no median area of naked skin proximally to it, the median and lateral scales mentioned above being present. In dried skins of adult examples of *M. javanica* the pad is as well developed as that of the young and similar to it.

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In the young example of *M. pentadactyla*, of approximately the same age as the young *javanica*, there is no true pad, the tail being scaly to the end beneath, although the scales at the extreme tip are much smaller and less distinctly horny than the rest and separated by naked skin. But in dried skins of adults a pad similar in shape to that of *javanica* is present; it does not, however, consist of smooth skin as in that species but is beset with minute scale-like roughnesses.

In some dried skins of young examples of *M. crassicaudata* the tip of the tail beneath is like that of the young example of *pentadactyla*, there being no true pad, but in adult examples the pad is absent, its place being taken by a median horny scale, as hard and compact as the other scales. Thus Matschie's statement that this species has a caudal pad is erroneous, as Anthony has shown (Bull. Mus. Paris, xxv. p. 20, 1919). The two large African species, *M. gigantea* and *M. temminckii*, have no pad, according to Matschie and Anthony. In most of the dried skins I have been able to see the scaling at the tip of the tail has been destroyed by the skinning; but my observations confirm Matschie's statement on that head.

There are some interesting facts to record in connection with the length and breadth of the tail. In *M. longicaudata* and *tricuspis* this organ is comparatively narrow and exceedingly long, longer indeed than the head and body combined, sometimes nearly twice as long. In the other species it is shorter than the head and body, although only slightly so sometimes in *M. javanica*. Thus in the length of the tail, as in the presence of the unscaly terminal pad, and the structure of the hind feet, *M. javanica* comes nearer to the long-tailed African forms than do the others. *M. pentadactyla* has a shorter tail and a less well-developed terminal pad than *M. javanica*; but whereas in the latter the sides of the tail gradually converge from the base to the tip, in *M. pentadactyla* the even convergence of the sides ceases before the extreme end, which is almost parallel-sided and more subcylindrical, suggesting greater prehensile skill. *M. crassicaudata*, generally at all events, has a shorter and broader tail than *M. pentadactyla* without a pad, but its sides evenly converge to the tip as in *javanica*. In the structure of the tail and of the hind feet it comes nearer the large African species, in one of which, *M. temminckii*, the tail is so broad as to have been described as paddle-like.

The Anal and Genital Area.

In examples of the species examined the anus opens in the centre of a well-defined eminence, and in adults and sub-adults it is sunk within a depression formed by the overfolded edges of the circumanal area. This eminence is mainly due to the presence of a pair of large anal glands, opening at the sides of the anus well within the depression, which probably acts as a

reservoir for their secretion. A strong repulsive odour which I noticed in a living example of *M. tricuspis* probably emanated from these glands. The external genital organs both of the male and female are situated on the anterior part of the anal eminence.

Text-figure 12.
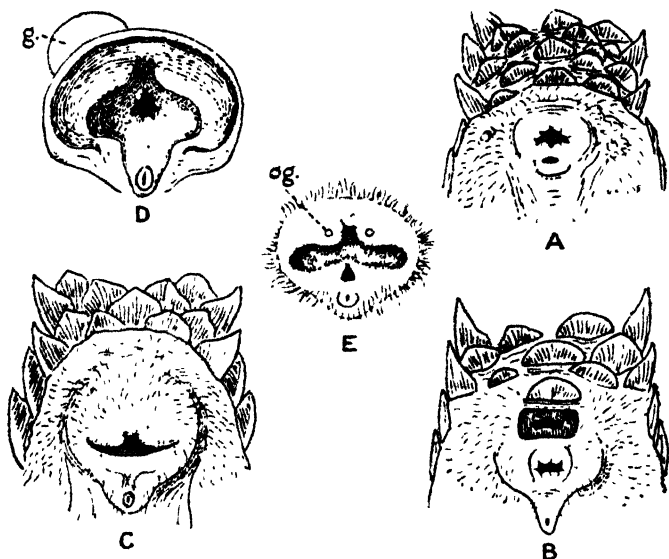
A. Anal and genital area of female *Manis javanica*.

B. The same of young male *M. pentadactyla* from Nepal, showing especially the oblong, probably glandular, depression behind the anal eminence and the disarrangement of the scales on the base of the tail.

C. The same of adult male *M. tricuspis*, showing the wide orifice of the anal sac.

D. Anal sac of the same species dilated to show the insunk anus and one of the anal glands (*g*) dissected.

E. Anal sac of female *M. tricuspis* expanded to show the orifices of the anal glands (*og*) and below the sac the vulva and clitoris.

In *M. tricuspis* the anal depression is well defined both in the male and the female, and when closed its orifice forms a transverse cleft. There is no depression on the hairy integumental area between the eminence and the base of the tail : and the first row of scales on the latter forms an evenly curved transverse line. The penis is a short, conical process projecting from the fore part of the eminence, and the orifice of the small glans may be seen surrounded by the prepuce. The perinæal area is short.

In the female the vulva opens just in front of the anal depression, and beneath it there is a small bilobed clitoris. In this sex also the perinæum is short.

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In a young male of *M. pentadactyla* there is also a distinct
anal eminence with the anus opening upon it; and just in front
of the anus there is a short projecting penis, which, however, is
much slenderer than in the specimen of *M. tricuspis* examined.
Just behind the anal eminence there is a very distinct trans-
versely oblong pit, about half the width of the eminence and
showing a marked depression in its centre. This is probably
glandular *. The scales at the root of the tail do not form an
evenly curved line owing to the forward shifting of the median
scale of the first row out of line with the two adjoining scales,
so that it lies just behind the pit above mentioned and probably
acts as a lid to it when the tail is lowered.

In a sub-adult male of *M. javanica* from Chantaboon, Siam
(*S. S. Flower*), the anal eminence is very pronounced, and the
anus itself is sunk in a deep depression formed by a thick
muscular projecting ridge arising from the circumanal area.
The orifice of this depression when close forms a transverse cleft,
suggesting a very large anal orifice. From the anterior end of
the margin of this depression depends the short simple penis.
The anal eminence is defined behind by a transverse externally
curved groove ; but there is no depression behind it such as is
seen in the young example of *M. pentadactyla*. The first row of
scales at the base of the underside of the tail forms an evenly-
curved series.

In a young female example of *M. javanica*, there is a com-
paratively low anal eminence; the anus in its centre is not
insunk and the vulva, a transverse slit, lies just in front of it.
There is no pit behind the anus, and the first row of scales of the
tail forms an evenly curved line defining the postanal area.

The observations above recorded, especially those relating to
the probably glandular postanal pit and the disarrangement
of the scales of the first row on the tail in *M. pentadactyla*, call
for further examination of the anal and genital regions on fresh
material, not only of the species here described but of *M. crassi-
caudata*, *M. temminckii*, and *M. gigantea*.

The Classification and Generic Nomenclature of the Pangolins.

From the preceding account it will be seen that the nature of
the variations in the external characters of the Manidæ are in
many cases of greater than specific value according to modern
standards.

1. The small, long-tailed West African species, *M. longicaudata*
and *tricuspis*, differ from the rest in the structure of their front
and hind feet. There are minor differences as well, such as the
great length of the tail, the development of its terminal pad, etc.,
associated no doubt with the essentially arboreal habits of the
animals. But the structure of the feet alone is quite sufficient

* Traces of this pit are observable in some dried skins of adult and young males
of this species.

to justify their separation from the rest. The two species in question are, moreover, so different from each other in scale-armature that they were given subgeneric rank by Gray, and full generic rank by Fitzinger.

2. In general form, appearance, and habits, as well as in the structure of their feet, the species mentioned in the last paragraph are strikingly distinct from the two large, heavily-built terrestrial species, *M. temminckii* and *M. gigantea*, of the same continent. Nevertheless, the four African species resemble each other, and differ from the Asiatic species in four characters, which compel the belief that they belong to the same stock. These characters are:— (1) the prodigious elongation of the xiphisternum into two branches extending backwards to the posterior ribs *; (2) the duplication of the median line of scales on the upper surface of the tail; (3) the absence of bristles protruding between the scales; (4) the total suppression of the pinna of the ear. Of these characters those supplied by the xiphisternum will appeal most strongly to anatomists as evidence of kinship; but the seemingly functionless arrangement of the caudal scales is a specialization perhaps as cogent on that head as any.

In the Asiatic species, on the contrary, the xiphisternum is comparatively short, and ends in an expanded plate shaped something like the blade of a spade, the median line of scales is typically continued uninterruptedly to the end of the tail, there are bristles projecting beneath the scales †, and the pinna of the ear is retained either as a definite ridge, or a comparatively large flap. It is perhaps needless to point out that in these characters the Oriental species form the more primitive group, and this points to Asia, and not Africa, as the original home of the order.

3. In the case of the three Asiatic species, although *M. pentadactyla* is in some respects intermediate between *M. crassicaudata* and *M. javanica*, it differs from both in the large size of the pinna; and, apparently, in the presence, in the male at least, of the postanal glandular depression, not to mention the peculiar narrowing of the distal end of the tail. Setting this species on one side, *M. crassicaudata* and *javanica* differ considerably from one another in habits, general form, in the structure of the hind foot, and in the absence in the former, and the presence in the latter, of the caudal pad; and since it may be confidently anticipated that other differences between these three Asiatic species will be revealed when properly pre-served material in alcohol is available for examination, I propose to assign them to three distinct genera.

It remains now to be seen what names are available for the genera I propose to admit.

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* Max Weber, Zool. Ergebn. einer Reise Nederl. Ost-Ind. ii. pp. 79-86, pl. ix. figs. 63-66. In the explanation of this plate, fig 64 is labelled by error *macrura* instead of *crassicaudata*, *macrura* being a synonym of *longicaudata*.

† Often rubbed off or shed in old specimens.

The two earliest names are *Manis* Linn. (Syst. Nat. ed. 10, p. 36, 1758), based upon *pentadactyla* * and *Pholidotus* Brisson (Regn. An. iii. Quadr. p. 19, 1762), comprising *pentadactyla*, cited by reference, and *longicaudata*, a new species.

Longicaudata was subsequently renamed *tetradactyla* by Linnæus (Syst. Nat. ed. 12, p. 53, 1766). I do not know why

Text-figure 13.
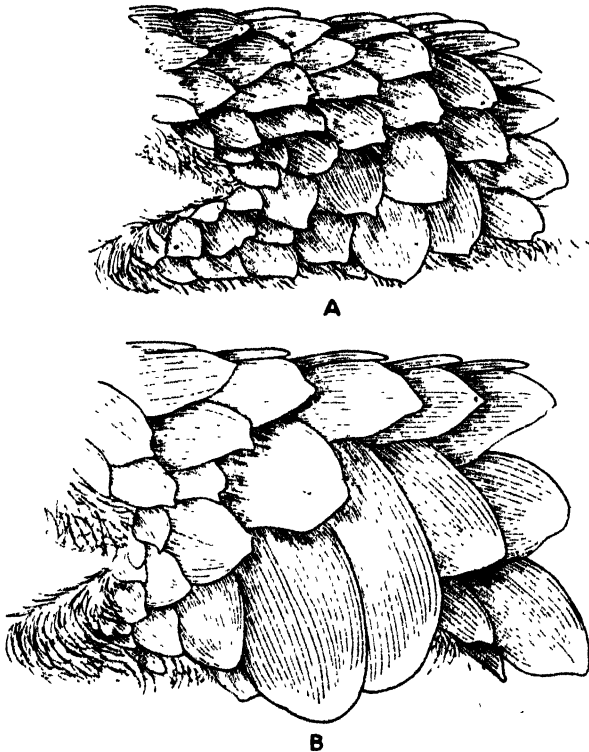
A. Side view of shoulder and part of the neck and fore leg of *M. tricuspis*, showing the comparatively small, numerous scales.
B. The same of *M. longicaudata*, showing the enlargement and reduction in number of the scales.

Matschie and Trouessart adopted Linnæus's name instead of Brisson's, which has four years' priority.

Two new subgeneric names were introduced by Rafinesque in

* Shown by Thomas (Proc. Zool. Soc. 1911, p. 133) to be the same as the Chinese and North Indian form, better known as *aurita*, and not, as was supposed, the same as the species of Peninsular India and Ceylon, which now takes the name *crassicaudata*.

1821 (Ann. Sci. Phys. Brux. vii. pp. 214–215*). With a clear perception of the value of the distinguishing characters between the five-toed and four-toed species, he subdivided *Manis* into two subgenera, *Pangolinus* for *pentadactyla* Linn. and *brachyura*, and *Phataginus* for *tricuspis* and *ceonyx*, two alleged new species, although *ceonyx* from the reference to its large scales is evidently a synonym of *longicaudata* Briss. These two subgenera he designated also by the trivial names Pangolin and Phatagin.

An advance in the classification was made by Sundevall in 1843 (K. Vet.-Akad. Handl. lxiii. pp. 245–281), when he divided the known species of *Manis* into three subgenera, restricting *Manis* to *longicaudata* and *tricuspis*, *Pholidotus* to *aspera* (= *javanica*), *javanica*, and *dalmanni* (= *pentadactyla*), and proposing the new name *Phatages* for *laticauda* (= *crassicaudata*) and *temminckii*.

With certain additions and emendations Gray's classifications of 1865, 1869, and 1873 were amplifications of the systems of Brisson, Linnæus, Rafinesque, and Sundevall. He divided the family into two main sections typified respectively by the manifestly five-toed and the apparently four-toed species after the manner of Brisson, Linnæus, and Rafinesque: and, following Sundevall, he restricted *Manis* to the four-toed forms, comprising *longicaudata* (= *tetradactyla*) and *tricuspis*; and *Pholidotus*, broadly speaking, to the five-toed species, including of course *pentadactyla*, giving full generic rank to them. In this he was followed by Fitzinger in 1872, and, in effect, by Trouessart in 1899 and 1905, although the latter regarded the two groups as of subgeneric value.

There are two cardinal points to notice in these classifications :—(1) the allocation of the name *Manis* to the four-toed species was clearly inadmissible, since that name was based in 1758 upon *M. pentadactyla* alone ; (2) as regards *Pholidotus*, Sundevall (and following him Gray, Fitzinger, and Trouessart) was acting quite within his rights in applying it to the first of the five-toed species assigned to it by Brisson. His action in so doing was tantamount to selecting *pentadactyla* as its type. But the actual and verbal selection of *pentadactyla* as the type of *Pholidotus* was apparently left to Trouessart in 1905†. To the further subdivision of the five-toed species I shall return presently.

Reverting to the four-toed group, Gray, appreciating the differences between the two admitted species *longicaudata* and

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* A rare work to which few systematists apparently have had access. The volume bears the date 1820; but, according to Mr. C. D. Sherborn, it was not published until a year later.

† It is true that in 1901 (Fauna of S. Africa : Mammals, ii. p. 216), W. L. Sclater selected *tetradactyla* as the type of *Pholidotus*. But herein he ignored the previous restriction by Sundevall and others of that name to *pentadactyla* and its allies. Moreover, he assigned *Pholidotus* to Storr 1780, not to Brisson 1762; but since Storr quoted no specific name under that title, neither *tetradactyla* nor any other species can be its type, assigning the name to him. On all counts, therefore, Sclater's action may be dismissed as invalid.

tricuspis, although referring both to the genus *Manis*, restricted the latter term in a subgeneric sense to *longicaudata*, and adopted as a subgenus for *tricuspis*, *Phatagin* of Rafinesque, taking, with characteristic perversity, that author's French rendering of the title *Phataginus*. Fitzinger also perceived the striking differences between these two forms, and while following Gray in assigning *longicaudata* to *Manis*, introduced the new name *Triglochinolophis* as a substitute for *Phataginus*.

Thus of the two long-tailed arboreal W. African forms, the small-scaled species *tricuspis* has three names—*Phataginus* Raf. 1821, *Phatagin* Gray 1865, and *Triglochinolophis* Fitz. 1872, whereas the large-scaled species, *longicaudata*, is without generic or subgeneric title, *Manis* being inadmissible for it. Since this form appears to me to deserve generic rank, I propose *Uromanis* for it.

To the five-toed species a considerable number of generic or subgeneric names have been applied.

Manis Linn., with type *pentadactyla*, takes *Pholidotus* Briss. as a synonym; and to this may be added *Pangolinus* Raf. with the same type, and *Pangolin* Gray with type *dalmanni* (= *pentadactyla*).

Phatages Sundevall contained the Indian species *laticauda*, and the African species *temminckii* as stated on p. 258 of his treatise; but on p. 273 Sundevall definitely cited *laticauda* as its type. An older name for this species is *crassicaudata* Geoff. St. Hilaire. To the synonymy of *Phatages* must be added *Phatagenus* supplied by Sundevall as an alternative.

Thus two of the admitted Asiatic species are already suited with names. But since there appears to be no available title for the third, *javanica*, I propose *Paramanis* for it.

Smutsia was applied by Gray in 1865 to *temminckii*, one of the two large African forms; and since the other, *gigantea*, appears to be congeneric with it, I assign both to that genus.

Thus the generic names with their synonymy and type-species will apparently be as follows:—

1. *Manis* Linn.   Type *pentadactyla*.
    Syn. *Pholidotus* Brisson.   Type *pentadactyla*.
    „   *Pangolinus* Raf.   Type *pentadactyla*.
    „   *Pangolin* Gray.   Type *pentadactyla*.
2. *Phatages* Sund.   Type *crassicaudata* (= *laticauda*).
    „   Syn. *Phatagenus* Sund.   (Proposed as an alternative.)
3. *Paramanis*, nov.   Type *javanica*.
4. *Smutsia* Gray.   Type *temminckii*.
    This genus also includes *gigantea*.
5. *Phataginus* Raf.   Type *tricuspis*.
    Syn. *Phatagin* Gray.   Type *tricuspis*.
    „   *Triglochinolophis* Fitz.   Type *tricuspis*.
6. *Uromanis*, nov.   Type *longicaudata*.

The characters of these genera may be tabulated as follows. —

a. Xiphisternum short, spade-like, the blade with convex posterior edge and forwardly directed spiniform anterior angles ; typically with a single median series of scales on upper side of posterior end of tail ; hairs projecting between the scales of the head, body, and limbs, except in old animals : pinna of ear at least represented by a thickened rim of integument. Subfam. *Maninæ.*

  b. Pinna of ear represented by a well-developed flap of flexible integument ; a definitely circumscribed deep, probably glandular, depression behind anus in male   .   ..   *Manis.*

  b'. Pinna of ear represented by a rim of thick skin ; no definite pit above anus in male.

    c. No terminal membranous pad at apex of tail beneath ; fore foot with pad poorly developed, its claws very long ; hind foot with claws short and blunt, projecting to a comparatively slight extent beyond the pad   ...   *Phatages.*

    c'. A terminal membranous pad on apex of tail beneath ; fore foot with well-developed pad, its claws shorter ; hind foot with claws comparatively long, about as long as those of the fore foot and projecting well beyond the pad   *Paramanis.*

a'. Xiphisternum produced into two long rods running back to the posterior ribs ; scales on upper side of apex of tail irregularly paired ; no hairs projecting between scales ; pinna of ear absent.

  d. Digit 1 of fore and hind foot as large as digit 5 and approximately on a level with it : digit 5 much smaller than digit 4 ; hind foot without expansion of sole behind digit 1, its claws short and blunt ; upper side of fore foot scaly to the claws ; body heavy, tail short, without terminal pad. (Terrestrial species.) Subfam. *Smutsiinæ.*   *Smutsia*

  d'. Digit 1 of fore and hind foot very small, set far behind level of digit 5, which is much larger than it and approximately in line with digits 4, 3, 2 ; hind foot with distinct expansion of sole behind digit 1, its claws long and sharp ; upper side of fore foot without scales ; body light, tail very long, with well-developed terminal pad beneath. (Arboreal species.) Subfam. *Uromaninæ*

    e. Scales small and numerous, the two inferior post-scapulars not markedly enlarged   .   *Phataginus.*

    e'. Scales very large and comparatively few in number, the two inferior post-scapulars enormously large, markedly larger than the next *   .   Uromanis.*

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* The elevation of the submarginal scales would seemingly increase to a considerable extent the width of the body in this Pangolin. Hence in the event of a fall from the tree-tops they might act like a patagium. The two large inferior post-scapular scales would be particularly efficacious in this respect.

30. The Comparative Anatomy of the Tongues of the Mammalia.—X. Rodentia. By CHARLES F. SONNTAG, M.D., F.Z.S., Anatomist to the Society and Demonstrator of Anatomy, University College.

[Received May 20, 1924. Read June 3, 1924.]

(Text-figures 31–38.)

Although the animals comprising the Order Rodentia are very diversified the lingual characters do not differ very much specifically. And all the tongues agree in being very thick. They all have short frena. The tongue fills the mouth closely, and it is in many cases divided into a low anterior part and a raised posterior intermolar eminence. The dorsum is frequently impressed by the palatal rugæ.

Family SCIURIDÆ (text-fig. 31)*.

The tongue is long, narrow, and thick, and is tapering or spatulate. The free part is moderately long, and the oral part comprises more than the anterior two-thirds of the dorsum. No intermolar eminence exists. The apex is rounded, but is devoid of a notch or large papillæ. The lateral borders are thick, and the lateral organs lie very far back owing to the great length of the

* The species examined by me were *Sciurus vulgaris, S. maximus, S. prevosti, S. hudsonius, S. palmarum, S. saltuensis bondæ, Finniscirrus leucostigma, Callosciurus notatus.* Tuckerman examined *Tamias striatus, Sciuropterus volucella, Arctomys marmotta, Cynomys ludovicianus.*

oral part of the dorsum. They have no large conical papillæ, but large fungiform papillæ are present in *Arctomys monax*. Median sulci are variable on both upper and lower surfaces of the tongue, but there is a median ventral ridge in *Sciurus prevosti*, *S. palmarum*, and *Callosciurus notatus*.

Circumvallate Papillæ:—The observations of Münch (**30**), Tuckerman (**42**), Owen (**32**), and myself have shown that there are without exception three circumvallate papillæ in a triangle with the apex directed backwards. They are richly supplied with taste-buds, and nerves have been traced into the epithelium.

Text-figure 31.
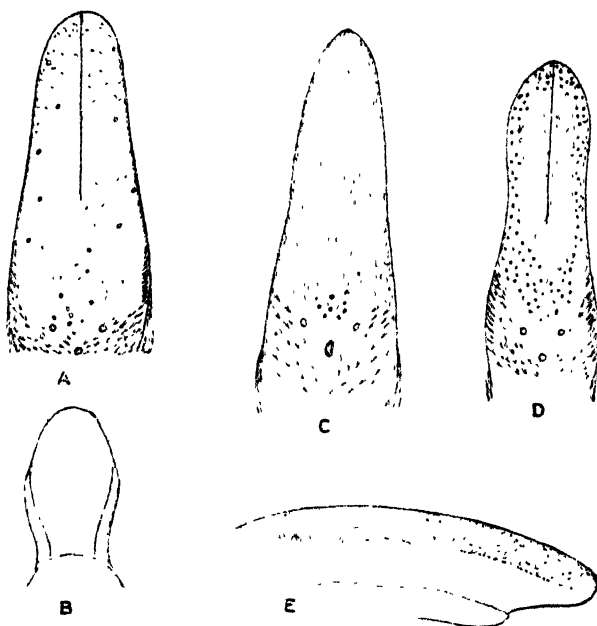
Tongues of the Sciuridæ. A. B. E: dorsum, under surface, and lateral view of tongue of *Sciurus palmarum*; C: *Sciurus prevosti*; D: *Sciurus saltuensis bondæ*.

Many glands open into the fossæ. The papillæ are circular or oval, and both forms may be present on the same tongue.

Fungiform Papillæ:—These papillæ are richly supplied with taste-buds, and they have the usual arrangement. There is, however, no thick cluster behind the apex of the tongue. They are scanty in *Sciurus vulgaris*, *S. prevosti*, *S. palmarum*, *Finnisciurus leucostigma*, and *Callosciurus notatus*. They form a thick cluster in front of the triangle of circumvallate papillæ in *S. saltuensis bondæ*. Authors who have described tongues other

than those examined by myself do not mention whether such a cluster was observed by them.

Conical Papillæ: —In all species they are numerous and close together. Those on the oral part of the dorsum are small, but those on the base of the tongue are large. They have the usual arrangement, and they are simple in character.

Lateral organs are present in all species. They have many taste-buds, and glands. They consist of six to nine laminæ separated by fissures of varying depth. The glands open on the summits of the laminæ in *Arctomys monax* (**40**), a very uncommon condition; but they open into the sulci in all other species. Owen (**32**) states that the Marmot is also peculiar in that its vallate papillæ are almost in line.

Glands: -No orifices were detected on the base of the tongue, but they may be very minute or concealed by overhanging papillæ. The mucous glands form a crescent on the base, and there are three groups of serous glands connected to the vallate triangle and lateral organs. The apical gland of Nuhn is absent.

There are no traces of frenal lamellæ, sublingua, plicæ fimbriatæ, lytta, or foramen cæcum, and this statement also applies to the tongues of the Castoridæ.

Family Castoridæ (text-fig. 32).

The tongue is relatively shorter, broader, and thinner than in the Sciuridæ, so the lateral borders are thinner and sharper. There is a low, broad pointed intermolar eminence, which extends right across the tongue in its posterior part. And there is a pronounced median ventral crest.

Circumvallate Papillæ: —Mayer (**27**) described two papillæ, but Munch (**30**), Tuckerman (**44**), and I observed three papillæ in a triangle with the apex directed backwards. Each papilla is circular in outline with a marked central pit, and its surface has many secondary papillæ. The fossæ are obvious, but the vallums are not very prominent.

Fungiform Papillæ: In contrast to the conditions in the Sciuridæ there are numerous, prominent, fungiform papillæ, and the prominence is due to the fact that the surrounding conical papillæ are very small and devoid of sharp points. There is a cluster in front of the intermolar eminence, and there is also a cluster on the eminence in front of the vallate triangle.

Conical Papillæ:—Those on the oral part of the dorsum are small, rounded, and closely set, and no pointed forms occur. They do not increase progressively in size from before backwards, but those in front of the vallate triangle are large. On the base of the tongue there are a few isolated papillæ.

Lateral Organs:—These structures cover an area of a half to two-thirds of each lateral border, so they are relatively larger than those of any other Mammal. Each consists of sixteen broad

laminæ separated by primary sulci and grooved by secondary fissures. Full descriptions have been published by Mayer (27), Boulart and Pilliet (2).

Glands :—The whole of the base of the tongue is covered with the orifices of mucous glands, and serous glands are connected as

Text-figure 32.
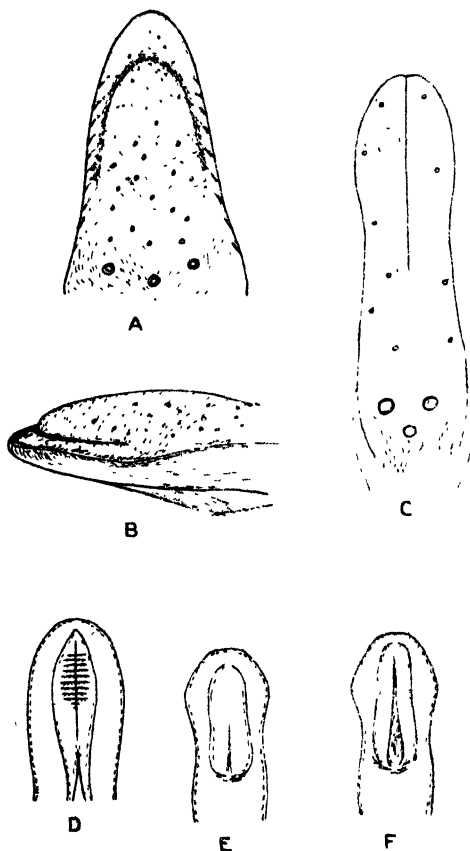
Tongues of the Castoridæ and Myoxidæ. A. B: dorsum and lateral view of the tongue of *Castor fiber*; C. D: dorsum and under surface of the tongue of *Myoxus dryas*; E. F: sublingua in *Myoxus glis* and *Muscardinus avellanarius*.

usual to the vallate triangle and lateral organs. The apical gland of Nuhn is present, and its opening is on the under surface of the apex of the tongue.

From the above it is evident that the tongues of the Castoridæ differ in many ways from those of the Sciuridæ.

Family M y o x i d æ (text-fig. 32).

The tongues are small, narrow, and thick, and the oral part comprises more than two-thirds of the dorsum.   The apex is rounded or truncated, and has neither a notch nor prominent papillæ of any kind.   The lateral borders are massive as in the Sciuridæ.   Sulci are present on the dorsum in *Myoxus dryas* and *Graphiurus crassicaudatus*.   The frenum is short, and there are no frenal lamellæ.

There are three circumvallate papillæ arranged in a triangle with the apex directed backwards, and their taste-buds are arranged in 4–6 rows.   The surfaces are granulated by secondary papillæ.   Fungiform papillæ are scanty, the conical papillæ are as in the Sciuridæ, and lateral organs are present in most species. Hönigschmied (**15**) stated that lateral organs are absent in *Muscardinus avellanarius*, but the organs are present in *Myoxus glis*; in the latter the taste-buds are disposed in 4–6 rows.

There is a well-developed sublingua.   It is a soft, flat plate extending backwards from the apex of the tongue to the frenum. The apex of the plate is bound down to the under surface of the apex of the tongue, so the whole organ resembles that in the Marsupialia.   This is the first time that the sublingua has been recorded in any Rodent.   The sublingua in three species is shown in text-fig. 32.

It is evident that the observations recorded above confirm the statement of Münch (**30**) that the Sciuroptera have three vallate papillæ in a triangle with the apex directed backwards.   They also show that the lingual characters are of value for purposes of classification (see page 739).

Family M u r i d æ (text-fig. 33)*.

The tongue is long, narrow, and thick, and it is tapering or spatulate.   The oral part is long and the base is short.   The apex is thick, rounded, and devoid of a notch or prominent papillæ of any kind.   There may be a median dorsal sulcus situated anteriorly.

There is an intermolar eminence in most species, and its characters differ.   In the Cricetinæ it is well marked in *Cricetomys*, but it is absent in *Cricetus*.   In the Gerbillinæ it is long, narrow, flat, and covered with papillæ.   In the the Arvicolinæ it is immense.   It is very variable in the Murinæ.   Thus it forms a considerable segment of a circle, and its surface is covered with innumerable small conical papillæ in *Mus musculus*; it is elongated with a rounded anterior extremity in *Mus barbarus*.

* The species examined were: Sub-family Cricetinæ—*Cricetus frumentarius, Cricetomys gambianus*; Sub-family Gerbillinæ—*Meriones schoushæi, Gerbillus ægyptius, G. shawi, G. pyramidum*; Sub-family Murinæ—several species of the genera *Sminthus, Isomys, Acomys, Mus, Arvicanthis, Pachiuromys, Epimys, Rattus*; Sub-family Arvicolinæ—*Arvicola, Fiber*.

M. blanfordi, Arvicanthis pumilio, and *Pachiuromys dupresi*; it is semicircular with a median sulcus in *Epimys namaquensis*; and it is absent in *Rattus rociferans.* The characters of the eminence in the Gerbillinæ are similar to those in *Mus barbarus.*

There is no trace of the foramen cæcum, sublingua, plicæ fimbriatæ, frenal lamella, lytta, or apical gland of Nuhn. The frenum is very short.

Circumvallate Papillæ:—Münch pointed out that the Muridæ are characterised by the presence of a single median circumvallate

Text-figure 33.
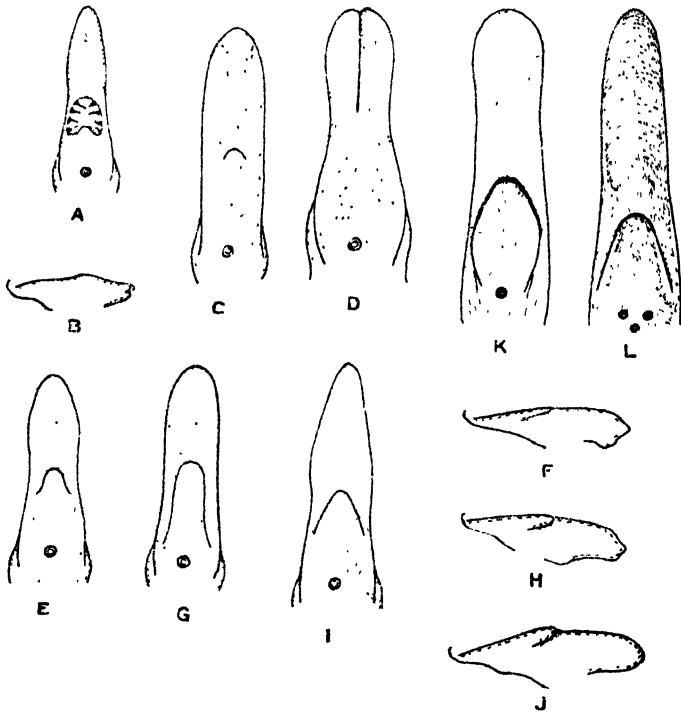
Tongues of the Muridæ, Spalacidæ, and Dipodidæ. A. B: dorsum and side view of
    the tongue of *Mus musculus*; C: *Mus barbarus*; D: *Cricetus frumentarius*; E. F: *Epimys*; G. H: *Gerbillus ægyptius*; I. J: *Dipus ægyptius*;
    K: *Arvicola*; L: *Rhizomys badius.*

papilla. And the only exception which I observed was *Cricetomys gambianus,* which has three circumvallate papillæ in a triangle with the apex directed backwards.

The single median papilla is usually of considerable size, and it forms a very obtrusive character on small tongues. It is rounded or flattened, and the surface is smooth or granulated by small secondary papillæ.

Podwisotzky (45) observed taste-buds on the upper surface of the papilla in some Muridæ, and Tuckerman (39) described how the taste-buds receive their nerves from a large, encapsulated ganglion in the papilla in *Fiber zibethicus*; he also counted the number of buds.

The *fungiform papillæ* are scanty, and it is sometimes difficult to detect them at all. In many species each papilla has a solitary taste-bud.

The *conical papillæ* are numerous, minute, and close together. Those on the base of the tongue may be larger than those on the oral part of the tongue. Their apices may be entire or bifid, and they are covered with strongly-cornified epithelium. Their numbers may be judged from Tuckerman's statement that there are 170 to the square millimetre in *Fiber zibethicus*.

Lateral Organs:—These structures are absent in *Cricetomys* and *Arvicola*, but they are present, though sometimes minute, in *Cricetus, Meriones, Gerbillus, Acomys*, and *Mus*. Honigschmied (15), contrary to my own observations, described organs in *Arvicola*. Many authors have given full accounts of the organs in *Mus*, and their statements have been collected by Oppel (31).

Family GEOMYIDÆ.

I did not have the opportunity of examining any material, but Tuckerman (44) observed a single vallate papilla in *Geomys bursarius*.

Family SPALACIDÆ (text-fig. 33).

In *Rhizomys* the tongue is long, narrow, and thick. It has a median dorsal sulcus anteriorly, and a low, flat, intermolar eminence posteriorly. There are three circumvallate papillæ in a triangle with the apex directed backwards. The lateral organs are small, and the fungiform papillæ are scanty. The conical papillæ are numerous, simple, and very close together; but those on the base of the tongue are not large. There are no traces of the foramen cæcum, frenal lamellæ, lytta, sublingua, or plicæ fimbriatæ.

Family DIPODIDÆ (text-fig. 33).

In the two species examined, namely *Dipus ægyptius* and *D. hirtipes*, the tongue is stumpy, narrow, thick, and pointed. The apex is devoid of a notch and prominent papillæ. And there is no median dorsal sulcus. The intermolar eminence is broad and covered with conical papillæ, which are very prominent in *D. ægyptius*.

Three circumvallate papillæ form a triangle with the apex directed backwards. The fungiform papillæ are scanty, and the conical papillæ are small all over.

48*

On the ventral surface of the tongue there is a central area bounded by lateral folds, which may represent plicæ fimbriatæ. The frenal lamella, foramen cæcum, lytta, and apical gland of Nuhn are absent.

As I have only had occasion to examine a single example of *Rhizomys*, the following remarks must only be regarded as provisional, and it may be necessary, should more material come to hand, to modify slightly the table of classification on page 739.

1. The Sciuromorpha, Spalacidæ, and Dipodidæ have three vallate papillæ in a triangle.

2. The Spalacidæ and Dipodidæ are distinguished from the Sciuromorpha by the presence of an intermolar eminence.

3. The Dipodidæ differ from the Spalacidæ in the dimensions of the conical papillæ, and in the presence of plicæ fimbriatæ.

Family OCTODONTIDÆ (text-fig. 34).

Species examined :—*Capromys fournieri, Myopotamus coypu, Ctenodactylus gundi.*

The tongues are long, tapering, and moderately thick. The apex is rounded or pointed, and is devoid of a notch and prominent papillæ. The free anterior part of the tongue is relatively thinner than in most Rodents. The lateral borders are thick, and have well-marked lateral organs on their posterior parts. There is a median dorsal groove situated posteriorly.

The intermolar eminence is well marked, and a deep, narrow groove encircles its anterior border in *Ctenodactylus gundi.* In *Myopotamus coypu* and *Capromys fournieri* the base of the tongue is thick, but there is no definite eminence.

The frenum is short, and there are no traces of frenal lamella, sublingua, plicæ fimbriatæ, foramen cæcum or apical gland of Nuhn.

Circumvallate Papillæ:—In all species there is a pair of papillæ. In *Capromys fournieri* and *Myopotamus coypu* they are both long and narrow, with their long axes directed backwards and inwards. Each has a median groove, and is surrounded by a well-marked fossa and vallum. The papillæ are placed far back, so the base of the tongue is very short. In *Myopotamus* the papillæ are more prominent than in *Capromys*. The type of papilla is very uncommon in the Mammalia, the only animals in which I have hitherto recorded it being the Tragulidæ (38). In *Ctenodactylus gundi* the papillæ are circular, and are relatively farther forwards than in the others. Consequently the oral and basal parts of the tongue are more evenly proportioned.

The fungiform papillæ are scanty and insignificant. The conical papillæ are numerous, small, and close together; and those on the base of the tongue are large. The lateral organs are composed of broad laminæ.

It is thus evident that the characters of the tongue separate *Ctenodactylus* from *Myopotamus* and *Capromys*. And the only difference between the tongues of these genera is the variation in

Text-figure 34.
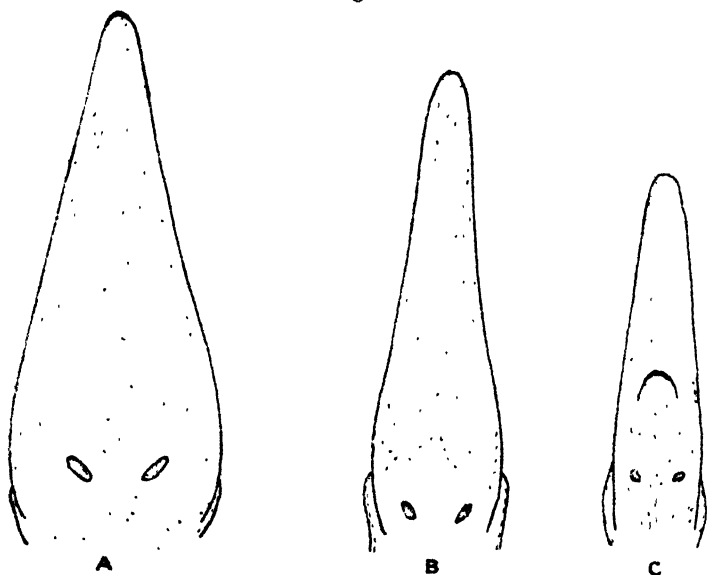
Tongues of the Octodontidæ. A : *Capromys fournieri* . B: *Myopotamus coypu*; C : *Ctenodactylus gundi*.

the prominence of the vallate papillæ. That is not a character which can be relied on, for the papillæ may shrink in preserving material.

Family H y s t r i c i d æ (text-fig. 35).

Zoological literature contains full descriptions of the tongues of several Hystricidæ. Thus the tongue of *Hystrix cristata* has been described by Mayer (**27**), Münch (**30**), Carus and Otto (**4**), Brücher (**3**), Cuvier (**5**), Leydig (**23**), and Parsons (**33**), that of *H. javanica* by Parsons, that of *H. prehensilis* by Carus and Otto, that of *Atherura africana* by Parsons, and that of *Erithizon dorsatus* by Mivart (**29**). For the purposes of the present paper I have examined tongues of all these species and that of *Sphingurus*.

In all cases the tongue is long, narrow, and thick and has two circumvallate papillæ. There are no traces of the foramen cæcum, lytta, sublingua, plicæ fimbriatæ, or frenal lamellæ.

The apex is rounded and may have a notch. In *Hystrix cristata* it bears long, pointed papillæ. There is a good median

dorsal sulcus on the anterior half of the tongue in the genus *Hystrix*; but there is no sulcus in *Erithizon*, *Atherura*, and *Sphingurus*.

The intermolar eminence is absent in *Hystrix* and *Atherura*, but it is very large in *Erithizon* and *Sphingurus*.

In *Hystrix* and *Atherura* there are peculiar structures on the anterior part of the dorsum. They take the form of flat, horny plates or of long processes. In *Hystrix prehensilis*, according to Carus and Otto (4), there are long processes, but in *H. cristata* and *H. javanica* there are flat serrated plates. In *Atherura* the plates may not be serrated at all. No traces of these structures exist in *Erithizon* and *Sphingurus*.

Text-figure 35.
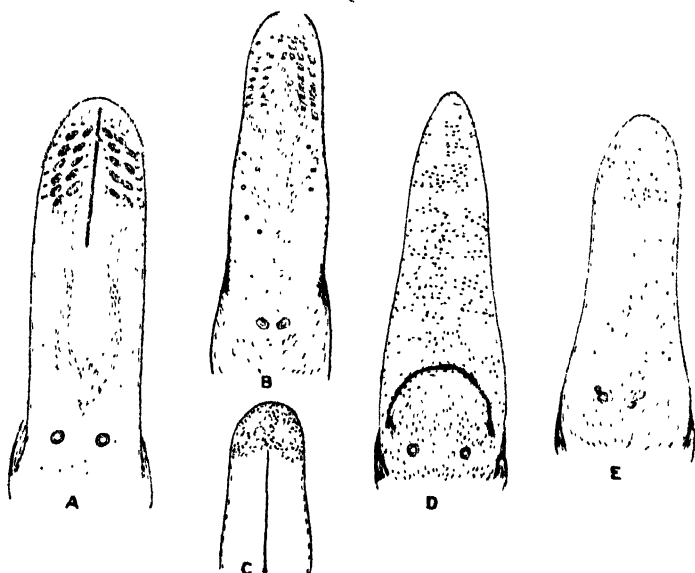
Tongues of the Hystricidæ. A: *Hystrix cristata*; B.C: dorsum and under-surface of the tongue of *Atherura africana*; D: *Erithizon dorsatus*; E: *Sphingurus prehensilis*.

The fungiform papillæ are most numerous in *Hystrix*, and the conical papillæ are numerous, simple, and close together.

Lateral organs are well developed in *Hystrix* and *Atherura*. In the former there are 16–20 sulci, and in the latter 10–12 sulci. No organs are present in *Erithizon* and *Sphingurus*.

It is thus evident that the tongues fall into two groups, the first containing *Hystrix* and *Atherura*, and the second including *Erithizon* and *Sphingurus*. It is, moreover, easy to distinguish between *Hystrix* and *Atherura*, but it is practically impossible to tell the tongue of *Erithizon* from that of *Sphingurus*.

Family CHINCHILLIDÆ (text-fig. 38).

The only species of which I was enabled to examine the tongue was *Lagostomus trichodactylus.* The tongue is long, narrow, and thick. The apex is rounded, massive, and devoid of a notch and prominent papillæ of any kind. The lateral borders are massive, but they have no traces of lateral organs. There are no traces of median dorsal sulci, foramen cæcum, sublingua, plicæ fimbriatæ, lytta, or frenal lamellæ. There are two circumvallate papillæ. The fungiform papillæ are very scanty, and the closely-set conical papillæ are best marked on the anterior part of the tongue. There are no large conical papillæ on the base of the tongue.

Family DASYPROCTIDÆ (text-fig. 36).

In *Cœlogenys paca* the tongue is thick with a very well-developed intermolar eminence. There is a good median dorsal sulcus on the anterior half of the tongue, and an equally well-marked median ventral sulcus runs along the entire length of the free part of the tongue. Several small transverse sulci pass out

Text-figure 36.
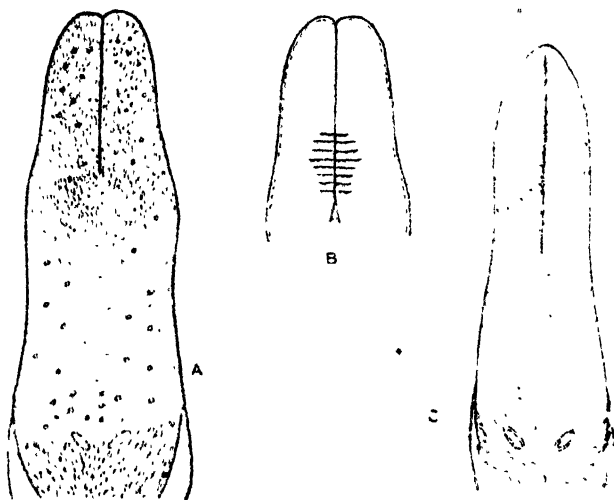
Tongues of the Dasyproctidæ. A. B : dorsum and under surface of the tongue of *Cœlogenys paca* ; C : *Dasyprocta prymnolopha.*

from the ventral sulcus. There is no trace of the foramen cæcum, sublingua, plicæ fimbriatæ, frenal lamellæ, or lytta. The apical notch is well marked, for the median dorsal and ventral sulci are quite continuous.

Papillæ:—There are two long, narrow circumvallate papillæ, whose long axes run forwards and outwards, but the fossa and vallum are indistinct. The fungiform papillæ are scanty, most lying behind the apex on the dorsum of the tongue. The conical papillæ are innumerable, simple, and closely set, and give a finely granular appearance to the dorsum. Those situated anteriorly are of moderate size, but those on the base of the tongue are very large. The lateral organs consist of rows of broad, flat laminæ separated by straight or V-shaped sulci, and a few secondary sulci traverse the laminæ.

Mayer (**27**) described conditions similar to the above.

In *Dasyprocta* the tongue is in most respects similar to that in *Cœlogenys*, but it has no median ventral sulcus.

Family CAVIIDÆ (text-figs. 37 and 38).

The tongues differ in shape from those in the other Hystricomorpha. They are long, narrow, and thick in the anterior half, but they are wide and thick posteriorly where the intermolar eminence lies. The tongue of *Hydrochœrus* differs from those of *Dolichotis* and *Cavia* in its absolute size, for it is the largest Rodent tongue. There are no traces of the foramen cæcum, frenal lamellæ, lytta, sublingua, or plicæ fimbriatæ.

The apex is rounded and has neither a notch nor prominent vallate papillæ of any kind. The lateral borders are massive, especially posteriorly, and have well-marked lateral organs. No median dorsal sulci are present on either surface of the tongue, but a transverse sulcus encircles the anterior border of the intermolar eminence in some species.

The *intermolar eminence* is immense and makes the posterior part of the tongue very thick and wide. It is covered with innumerable papillæ. None of these papillæ are very large in *Dolichotis* and *Hydrochœrus*; but they are large and pointed and give the front of the eminence a very serrated appearance in *Cavia*. In the latter there are concentric circles of large papillæ on the eminence.

Papillæ:—In none of the numerous tongues examined by myself were there any circumvallate papillæ like those of the majority of Mammals. The appearances were like those in some Odontoceti (**38**), but the microscopic structure differs. They consist of laminæ separated by sulci, so they resemble the lateral organs on the same tongue. The following arrangements occur:—

1. *Dolichotis* :—One lamina with two sulci on each side.
2. *Hydrochœrus*:—One or two laminæ on each side.
       Two laminæ on the right and three on the left (Münch, **30**).
3. *Cavia* :—Two laminæ on one side and three on the other.
       Three laminæ on one side and five on the other (Hönigschmied, **17**).

The observations of several authors on the histology of the epithelium and on the regeneration of the gustatory organs after injury have been collected by Oppel (**31**).

The fungiform papillæ are scanty, but are present on the sides of the dorsum, both on and in front of the intermolar eminence.

The conical papillæ make the tongue in front of the intermolar eminence rough, although they are not very large. The genus *Cavia* stands out from the others by the presence of the large papillæ on the front of the eminence.

Text-figure 37.
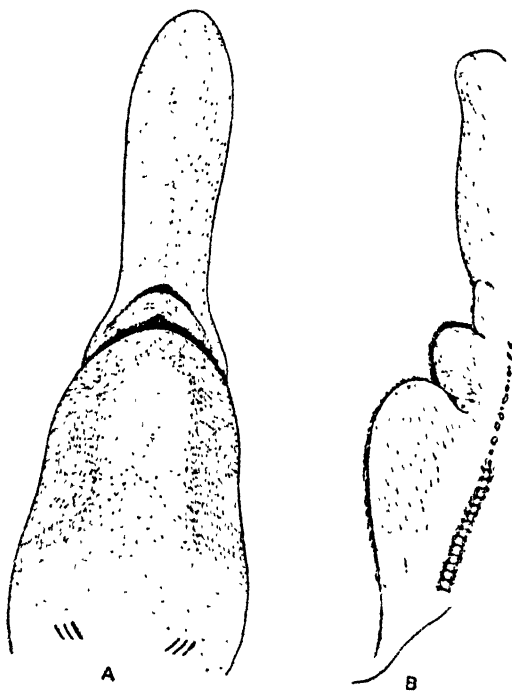
The tongue of *Hydrochœrus capybara*. A : dorsum ; B : lateral view.

The *lateral organs* are well marked in every case. They consist of many laminæ separated by sulci. They are placed low down on the sides of the tongue, or they are tucked away under the overhanging edges of the intermolar eminence. Sometimes they have a plate-like appearance.

v. Ajtai (**1**) stated that there are no lateral organs, but v. Ebner (**6**), Podwisotsky (**45**), Hönigschmied (**17**), and I observed them clearly.

The glands in *Cavia* have been described in detail by Podwisotsky (**45**), and v. Ebner (**6**), and I have nothing to add to their full accounts.

Text-figure 38.
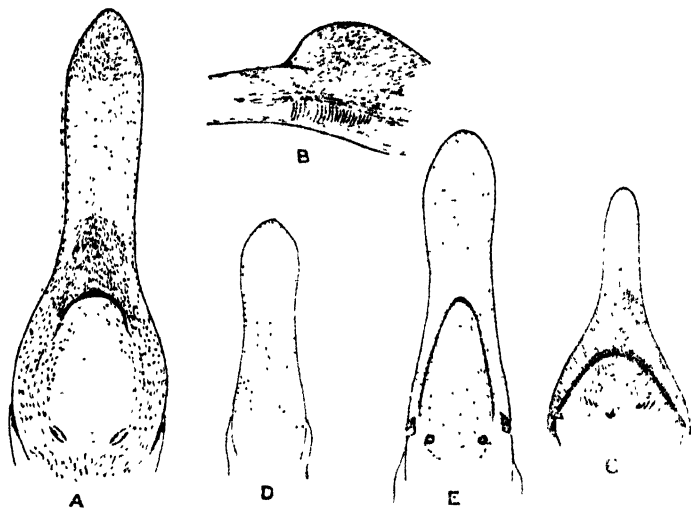
Tongues of the Caviidæ, Chinchillidæ, and Leporidæ. A. B : dorsum and lateral view of the tongue of *Dolichotis patachonica* ; C : *Cavia cobaya* ; D : *Lagostomus trichodactylus* ; E : *Lepus cuniculus.*

It is thus evident that the lingual characters are of value in the classification of the genera *Cavia*, *Hydrochœrus*, and *Dolichotis*. I have not had tongues of *Cerodon* for examination.

Family LEPORIDÆ (text-fig. 38).

As there are very many accounts of the tongue of the rabbit, I only append the following list of characters :—

1. Tongue spatulate.
2. Intermolar eminence long, prominent, pointed, and narrower than the tongue.
3. Two vallate papillæ.
4. Fungiform papillæ scanty and minute.
5. Conical papillæ minute.
6. Lateral organs form prominent swellings.

CLASSIFICATION.

From the data given above it is evident that the value of the lingual characters for taxonomic purposes is very variable. Each family has its own characters, but it is only in the Myomorpha

and Hystricomorpha that the genera have distinctive lingual characters. The systematic arrangement of the tongues is as follows :—

I. Three circumvallate papillæ in a triangle.

    A. Sublingua present... .. ..   MYOXIDÆ.

    B. Sublingua absent.

        a. No intermolar eminence ; conical papillæ on base of tongue
        long ; no apical gland of Nuhn ; lateral organs less than
        half length of tongue ...   .   SCIURIDÆ.

        b. Large intermolar eminence; conical papillæ on base
        small ; apical gland present; lateral organs half length
        of tongue .   .   ..   CASTORIDÆ.

        c. Eminence well marked : conical papillæ small all over :
        lateral organs small ; no apical gland   . ...   SPALACIDÆ & DIPODIDÆ.

II. A single median circumvallate papilla .. ..   (In MURIDÆ only)

        a. No intermolar eminence; lateral organs small ... . .   *Cricetus.*

        b. Eminence small ; lateral organs absent   . .   ..   *Cricetomys.*

        c. Eminence moderate ; lateral organs small   ... .   *Mus, Acomys, Gerbillus,*
        Meriones.

        d. Eminence immense ; no lateral organs   ....   *Arvicola.*

III. A pair of circumvallate papillæ.

    A. Anterior part of tongue narrow, posterior part very broad.

        a. Tongue very large ; intermolar eminence has no large
        pointed papillæ   ....   *Hydrochœrus.*

        b. Tongue not very large.

            i. No large pointed papillæ on eminence   . ..   *Dolichotis*

            ii. Large pointed papillæ on eminence   . . .   *Caria.*

    B. Tongue tapering Intermolar eminence when present as
    wide as tongue.

        a. Conical papillæ small on base of tongue.

            i. Tongue very small .   .   .   *Lagostomus*

            ii. Tongue not very small.

                a'. Serrated plates on anterior part .. . . *Hystrix.*

                b'. Non-serrated plates on anterior part .   .. *Atherura*

                c'. No plates on tongue   . .. *Erithizon* and *Sphingurus.*

        b. Conical papillæ on base of tongue large.

            i. No median dorsal sulcus anteriorly ; lateral organs small.

                a'. Vallate papillæ circular ; eminence large.. .. .   *Ctenodactylus*

                b'. Vallate papillæ elongated ; no eminence ..... .   *Capromys* and
                Myopotamus

            ii. Median dorsal sulcus good : good lateral organs.

                a'. Median ventral sulcus present   .. ..   *Cœlogenys.*

                b'. No ventral sulcus   .. ..   *Dasyprocta.*

    C. Tongue spatulate. Eminence narrower than tongue. Large
    lateral organs .. ..   LEPORIDÆ.

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(Text-figures 39–44.)

Order MARSUPIALIA.

Sub-order Polyprotodontia.

The tongue is ovoid in shape, or it tapers gradually or rapidly from behind forwards. The free part is thin as in the Carnivora. The *apex* is rounded and devoid of a notch ; and it has prominent conical papillæ in *Metachirus opossum* and *Marmosa elegans*. No species has many fungiform papillæ on the apex. The *lateral borders* gradually thicken from before backwards. They have small conical papillæ in all species, but fungiform papillæ and lateral organs are variable. *Median sulci* are absent from both dorsal and ventral surfaces. At the posterior parts of the lateral borders there are comb-like or serrated ridges of mucous membrane in the genera *Didelphys, Dasyurus, Metachirus,* and *Perameles* ; but these structures are absent in *Sarcophilus, Marmosa,* and *Philander* ; they vary in appearance and in the extent to which they cross the dorsum of the tongue. There is no *intermolar eminence* in any species, but the *sublingua* is present in all.

Circumvallate Papillæ (text-fig. 39) :—From the writings of Poulton (18), Grant (6), Flower (3), Mayer (9), and Oppel (14), it appears that all tongues hitherto examined have three papillæ in a triangle with the apex directed backwards. In *Dasyurus riverrinus* and *Sarcophilus harrisi* I observed five papillæ in a V, but there were three papillæ in a triangle in *Didelphys azaræ, D. marsupialis, D. virginianus, D. quicka, Sminthopsis crassicaudata, Dasyurus maugæi, Thylacinus, Perameles obesula, P. nasuta, Matachirus opossum, Marmosa elegans,* and *Philander laniger.* There are differences in the shape of the triangle and in the characters of the papillæ, but in all species the two basal papillæ are small and the sopterior papilla is large.

The papillæ form an equilateral triangle in *Didelphys azaræ*, *D. marsupialis*, and *Perameles obesula*; they form an isosceles triangle in *Marmosa elegans* and *Philander laniger*; and they are nearly in line in *Metachirus opossum*.

Text-figure 39.
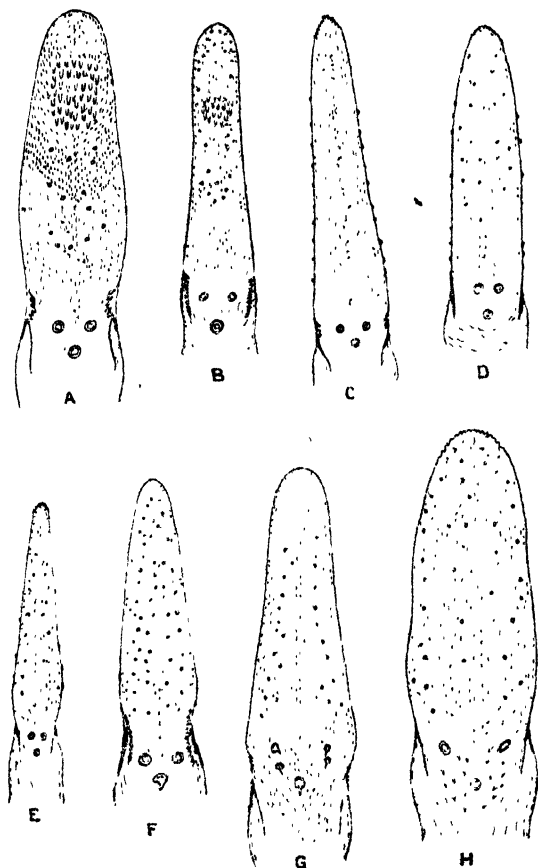
The tongues of *Didelphys azaræ* (A), *D. marsupialis* (B), *Metachirus opossum* (C), *Philander laniger* (D), *Marmosa elegans* (E), *Perameles obesula* (F), *Dasyurus viverrinus* (G), *Sarcophilus harrisi* (H).

The papillæ may have a flat surface when viewed from above, and there may be small secondary papillæ giving them a granular appearance. In *Dasyurus* they are drawn out into long points, which are directed backwards. Poulton (**18**) suggests that the surface, not being occupied by taste-buds, has been converted into

a large filiform papilla. Such an arrangement is unique. The fossæ may be closed or patulous and the vallum varies in prominence. Sometimes the vallum is cut up into lobules. The papillæ may be surrounded closely by conical papillæ, or they may be situated on a smooth area of mucous membrane.

When the papillæ are divided vertically it is seen how they are narrow at the points of attachment to the tongue. Consequently the fossæ pass downwards and inwards under the papillæ for a considerable distance. This gives the taste-buds a

Text-figure 40.
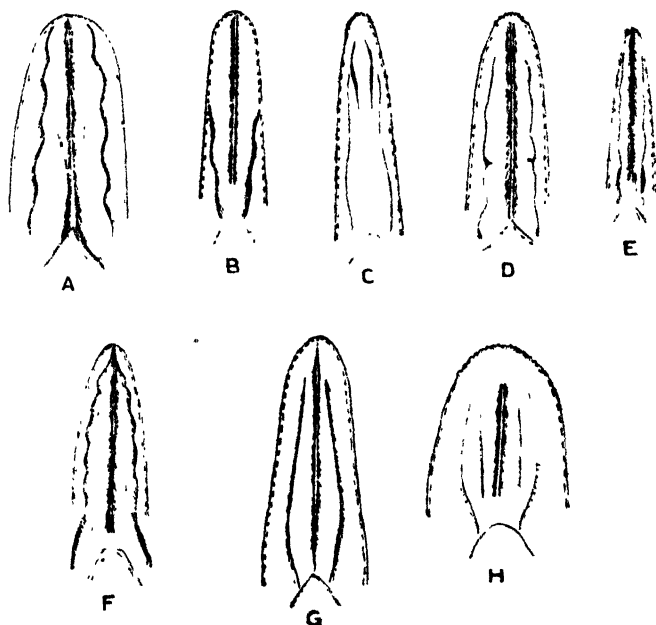
The sublingua in *Didelphys azaræ* (A), *D. marsupialis* (B), *Metachirus opossum* (C), *Philander laniger* (D), *Marmosa elegans* (E), *Perameles obesula* (F), *Dasyurus viverrinus* (G), *Sarcophilus harrisi* (H).

well-protected position, and the protection is still further increased by the power which the tongue possesses of closing the fossæ.

Fungiform Papillæ (text-fig. 39) :— These papillæ vary in numbers. In *Didelphys* there are a few scattered papillæ round the edges of the dorsum, and there are many behind the patch of large conical papillæ which occupies the anterior part of the dorsum. In *Dasyurus*, *Sarcophilus*, *Perameles*, and *Philander* they are very numerous and very small; in *Marmosa* they are likewise numerous, and they are relatively large; but they are scanty in *Metachirus*. The number of taste-buds in the fungiform

papillæ varies. Thus Oppel (14) found none in *Dasyurus hallucatus*, but many exist in *Sminthopsis crassicaudata*.

Conical Papillæ (text-fig. 39):—The various arrangements which are revealed when the tongue is examined through a powerful lens are shown in the figure. Poulton (18) laid great stress on types which he called respectively coronate and fasciculate papillæ. They are, however, present in animals belonging to other Orders.

In *Didelphys* alone there is a large area on the anterior part of the dorsum in which the papillæ have long, horny, straight or recurved processes. It is surrounded by a zone of small papillæ. This area resembles the area which is present in the Ailuroid Carnivora (26), which I previously called the spinous patch. It has relatively stronger papillæ in *D. azaræ* than in *D. marsupialis*. The region behind this patch is not divisible into zones as in the Ailuroidea.

When the relative sizes of the papillæ on the oral and pharyngeal parts of the tongue are compared it is seen how the latter are large in *Dasyurus*; they are of moderate length, but larger than the oral papillæ in *Sarcophilus*; and they are minute or absent, thus making the pharyngeal part almost or quite smooth in *Didelphys, Marmosa, Metachirus, Philander,* and *Perameles*.

In the region in front of the vallate area the papillæ are all small, but they are best marked in *Didelphys*.

In all species there is a zone of conical papillæ of differing width running round the circumference of the ventral surface; and the line of demarcation between it and the non-papillary part is marked.

Lateral Organs are absent in all specimens examined by myself. Oppel (14) mentions organs in *Sminthopsis crassicaudata*, and Tuckerman (20) describes them in *Didelphys virginiana*. Poulton (18) states that they are absent in *Perameles, Dasyurus,* and *Didelphys*.

Sublingua:—In all Polyprotodontia there is a very well-marked sublingua; and in no case is it reduced to the state of plicæ fimbriatæ. The median ridge is very obtrusive, the apex is adherent to the under surface of the apex of the tongue, and the thin lateral parts can be separated from the under surface of the tongue for a variable distance. The appearances in various species are shown in text-fig. 40. The features are very different from those in the sublingua of the Primates (23).

The *lytta* is entirely absent.

There is no trace of the foramen cæcum. The frenum is short, and there are no frenal lamellæ.

The chief points to note about the tongues of the Polyprotodont Marsupialia are:—

1. The thinness of the free part of the tongue.
2. The small size of the fungiform papillæ.

3. The basal vallate papillæ are smaller than the posterior one.

4. The absence of lateral organs.

5. The well-developed sublingua.

6. The taste-buds are well protected under the bases of the vallate papillæ.

Sub-order **Diprotodontia**.

The tongue has parallel sides, or tapers from behind forwards. The free part is thin, but it is relatively thickest in *Macropus*. The apex is round or pointed, and it has no large papillæ ; it has a median notch in *Trichosurus*. The lateral borders thicken progressively from before backwards, and lateral organs are present on their posterior parts in most species. There is no well-defined intermolar eminence, but the posterior part of the dorsum is slightly raised in *Macropus, Dendrolagus,* and *Cœnolestes.*

The median dorsal sulcus varies as follows :—

1. Sulcus does not reach apex of tongue—*Macropus, Dendrolagus, Phascolarctos, Pseudochirus, Cœnolestes.*

2. Sulcus reaches apex —*Trichosurus.*

3. Sulcus absent—*Petaurus,* some examples of *Phascolarctos.*

On the ventral surface there is to be found either a complete sublingua, or a strong median ridge representing it. The foramen cæcum, frenal lamellæ, and lytta are absent.

Circumvallate Papillæ (text-fig. 41) :—With the exception of *Phascolarctos cinereus,* which has one median papilla of moderate size, the Diprotodont Marsupials have three papillæ in a triangle with the apex directed backwards. Owen (15) observed one papilla in a specimen of *Macropus,* but that is unusual. The papillæ vary in prominence, for they may protrude beyond the vallum, or they may be retracted within the fossæ. The surface of the papilla is smooth or granular, and it may be drawn out into a point as in the case of *Dasyurus.* Poulton (18) points out that the apex may be turned forwards.

The triangle of papillæ may be equilateral or isosceles, so that the posterior angle may be open or acute. Poulton (18) arranged the tongues as follows :—

1. Angle open—*Halmaturus, Macropus, Petrogale.*

2. Angle acute—*Trichosurus, Petaurus, Acrobates.*

He found, moreover, that the papillæ are all identical in size in the former group, but the two anterior papillæ are smaller than the posterior papilla in the second group.

In the examples studied by myself the conditions of the posterior angle and the relative sizes of the anterior and posterior papillæ are as in Poulton's groups, and I must add *Pseudochirus* to the second group. Osgood's (22) illustration would place *Cœnolestes* in the first group.

Tuckerman (20) arranged the genera as follows :—

A. Papillæ concealed and ridge-like—*Macropus* and *Halmaturus*.

B. Posterior papilla as in higher Mammals. Anterior papillæ still in a transitional stage —*Trichosurus, Petaurus, Acrobates, Bettongia*, and *Phascolarctos.*

C. All papillæ as in higher Mammals—*Phascolomys.*

It will be noticed that Tuckerman observed three papillæ in *Phascolarctos*. Some observers, including myself, include *Phasco larctos* and *Phascolomys* in the same family, so the number of vallate papillæ is a differential character.

Tuckerman also grouped the Polyprotodontia with the Diprotodontia as follows :—

Group A.— *Dasyurus.*
     „   B.— *Didelphys.*
     „   C. — *Perameles.*

When a vertical section is made through the middle of the papillæ it is seen how they are cylindrical throughout or tapering, with the broad end above or below. In the last form the free end of the papilla may be pointed, flattened, or rounded. The point may be retracted within the fossa, or it may protrude. The last form is described as the Marsupial type. It has been shown by Poulton (18) and Tuckerman (20) that the papillæ in the Marsupials are transitional between those in *Ornithorhynchus* and those in the higher Mammals. The whole question of the evolution of the lingual structures will be described in the next and concluding paper of this series.

The taste-buds may be very numerous, and they may reach even on to the free surface of the papilla. The nerve to the taste-buds is very large.

Fungiform papillæ are not numerous, and, as in the Polyprotodontia, they are small. Many are concealed entirely among the long coronate and other mechanical papillæ. They are sessile or pedunculated, and many have taste-buds. Poulton regards the fungiform papillæ as tactile organs, and he does not consider them to be the same as those in higher Mammals.

The *conical papillæ* are mainly of three kinds :—

1. Simple hair-like papillæ.
2. Fasciculate papillæ.
3. Coronate papillæ.

Poulton (17) classified the tongues into two groups according to the presence of papillæ of the second type as follows :—

A. Coronate papillæ with irregular circles of secondary papillæ (in some places). Intercalated single hair-like papillæ are present—*Halmaturus, Macropus, Petrogale.*

B. Coronate papillæ less irregular. No intercalated single hair-like papillæ—*Petaurus, Trichosurus, Acrobates.*

There are no Diprotodonts in his third group in which the coronate papillæ are very regular, and there are no intercalated hair-like papillæ.

Much has been written about the arrangement and histology

Text-figure 41.
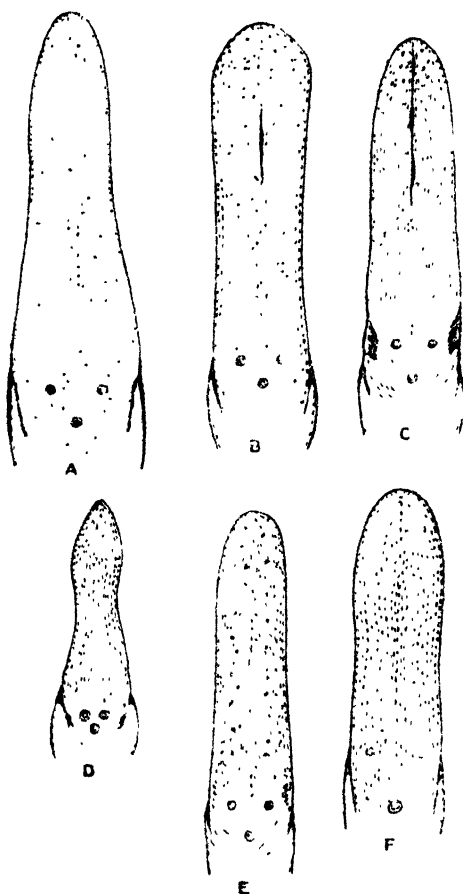
The tongues of *Macropus brunii* (A), *Dendrolagus ursinus* (B), *Trichosurus vulpecula* (C), *Petaurus sciureus* (D), *Pseudochirus peregrinus* (E), *Phascolarctos cinereus* (F).   (Some specimens have one vallate papilla.)

of the papillæ, and the observations of other authors have been collected by Oppel (**14**).

Lateral Organs:—These structures are very variable in the Diprotodonts, and they exhibit various stages in the evolution of

the organs in the higher Mammalia. The forms can be arranged in four groups:—

1. Organs absent—*Tarsipes* (**19**), *Phascolomys* (**14**), *Cœnolestes* (**22**). Some say they are also absent in *Phascolarctos*.

2. Organs very primitive, resembling the orifices of a row of gland ducts—*Halmaturus*..

3. Orifices closer and more slit-like—*Macropus*, *Epyprymnus*, *Petrogale*, *Pseudochirus*.

4. Organs have slits as in higher Mammals—*Trichosurus*, *Petaurus*, and *Acrobates*.

Text-figure 42.
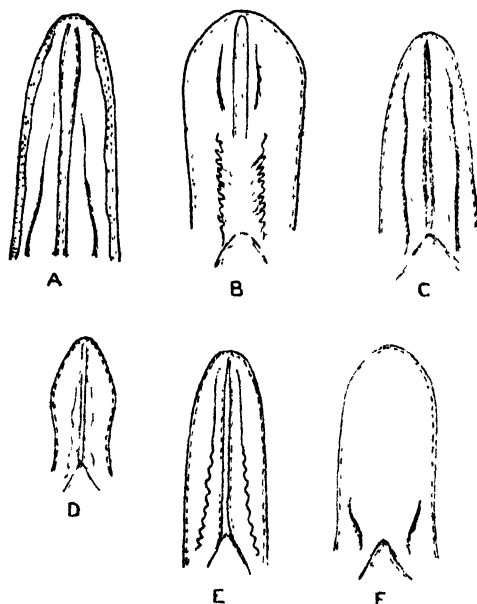
The sublingua in *Macropus brunii* (A), *Dendrologus ursinus* (B), *Trichosurus vulpecula* (C), *Petaurus sciureus* (D), *Pseudochirus peregrinus* (E), *Phascolarctos cinereus* (F).

When furrows are present, as in Group 4, glands open into their fundi. The evolution of the organs in the entire Mammalian Class will be described in the next paper of this series. Speaking generally, the simplest form is a gland duct with tastebuds in its wall, and the most complex is a furrow with buds on the sides and glands opening into the fundus.

Glands:—The serous glands form an area of varying shape stretching across the tongue from lateral organ to lateral organ and including the vallate area. In tongues without lateral organs

they simply form a central mass round the vallate area. The mucous glandular mass sends forwards two processes, which are best marked in *Phascolarctos*. Oppel (14) has shown these in coloured plates.

Sublingua:—The sublingua shows various degrees of reduction, and the median keel or plica fimbriatæ alone may be present. Gegenbaur (5) and Oppel (14) have described it in several forms, and the following list gives the arrangements observed by myself. They are shown in text-fig. 42.

1. Median keel and large lateral laminæ with entire edges reaching apex of tongue— *Trichosurus, Petaurus*.

2. Median keel and large lateral laminæ reaching apex of tongue. Edges crenated posteriorly—*Pseudochirus*.

Text-figure 43.
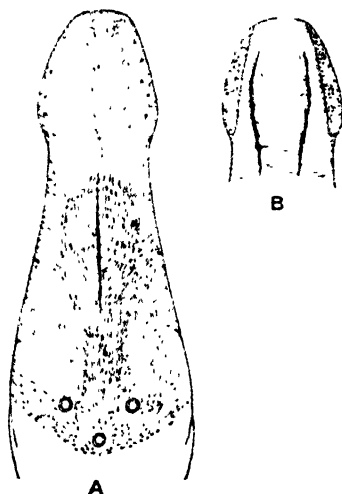
The tongue of *Phascolomys mitchelli* (dorsum and inferior surface).

3. Median keel and large lateral laminæ not reaching apex of tongue—*Dendrolagus*.

4. Median keel present. Laminæ reduced or absent—*Macropus*.

5. Plicæ fimbriatæ alone present—*Phascolarctos*.

6. No median keel. Sublingua soft and approaching the condition of plicæ—*Phascolomys*.

It is thus evident that the Koala and Wombat differ from other Diprotodonts in the state of the sublingua.

Osgood's account of *Cænolestes* (22) shows that the sublingua is included in the first or second group. In no case did I observe

the apex of the sublingua serrated as in some of the Polyprotodonts. In all forms the apex of the sublingua is bound down to the under surface of the tongue, and the whole structure is soft. It is a vestigial structure, and it performs no function. It has some resemblance to the sublingua in the Dormice (**28**), but it is different from that in the Lemuroidea (**23**).

The *lytta* is absent, and there is no trace of the *apical gland of Nuhn.*

Conclusions.

1. There are no characters which distinguish the tongues of the Polyprotodonts from those of the Diprotodonts.

2. The circumvallate papillæ form a triangle in the vast majority of cases. The papillæ form a series of stages which are transitional between the primitive type in *Ornithorhynchus* and that in the higher Mammalia. In many forms the papilla is drawn out into a point, and this appears to be a Marsupial characteristic.

3. Lateral organs are absent in all Polyprotodonts and in some Diprotodonts. In other Diprotodonts they exhibit stages in the evolution of the organs in the higher Mammalia.

4. The coronate papilla is universal in the Marsupialia, but it also exists in higher Mammalia.

5. The mass of mucous glands sends two processes forwards into the tongue. These are largest in *Phascolarctos.*

6. The sublingua is large in the Polyprotodonts, but it shows various degrees of reduction in the Diprotodonts.

7. The characters of the vallate papillæ and sublingua separate the Macropodidæ from the Phalangeridæ and Phascolarctidæ.

8. The lingual characters distinguish *Phascolarctos* from *Phascolomys.*

9. It is impossible to use the lingual characters alone for purposes of classification, for the arrangements of Poulton and Tuckerman described above show that both Polyprotodont and Diprotodont genera are mixed up together in each group. If, however, the Polyprotodonts are separated from the Diprotodonts by other anatomical characters the lingual features may be employed for taxonomic purposes as follows :—

Sub-order **Polyprotodontia.**

A. All vallate papillæ drawn out into points ... ... *Dasyurus.*
B. Papillæ not all drawn out into points.
    a. All papillæ as in higher Mammals.
        i. Fungiform papillæ and sublingua small... ... ... *Sarcophilus.*
        ii. Fungiform papillæ and sublingua large ... ... *Perameles.*
    b. Posterior papillæ only as in higher Mammals.
        i. Spinous patch on anterior part of dorsum ... ... *Didelphys.*
        ii. No spinous patch present.
            a'. Prominent papillæ on apex of tongue... ... ... *Marmosa, Metachirus.*
            b'. No prominent papillæ on apex... ... ... *Philander.*

Sub-order **Diprotodontia.**

A. Lateral organs absent.

    a. All papillæ drawn out into points . .   ..   *Cænolestes.*

    b. Posterior vallate papillæ as in higher Mammals; basal
        papillæ transitional . ... *Tarsipes, Phascolarctos.*

    c. All papillæ as in higher Mammals . ... *Phascolomys.*

B. Lateral organs present.

    a. Vallate papillæ concealed and ridge-like.

       i. Lateral organs like a row of ducts   ,.. .... *Halmaturus.*

      ii. Lateral organs more slit-like... .. .   ... *Macropus* and *Æpyprymnus.*

    b. Posterior papillæ as in higher Mammals; anterior papillæ
        transitional ..   .. .. *Trichosurus, Petaurus, Acrobates.* and *Bettongia.*

Order **MONOTREMATA.**

Much has been written about the tongues of members of this
Order, but there are still a number of facts to be recorded about
the macroscopic appearances.

The external appearances of the tongue in *Ornithorhynchus*
differ markedly from those in the Echidnidæ, for the organ has
undergone much specialisation in different directions in accor-
dance with the character of the food and the method of
preparing it for gastric digestion.

In *Ornithorhynchus* the tongue has the general appearance of
that in some Rodents. Thus it tapers from behind forwards,
and there is a large intermolar eminence stretching right across
the posterior part. This eminence is relatively larger than
in any other Mammal, and it bears two horny lingual teeth
on its anterior border. It is believed that these structures
direct insects into the cheek-pouches (text-fig. 44). The part
of the tongue in front of the eminence is covered with horny
retroverted papillæ, which are largest anteriorly; those in the
middle of the dorsum are very obvious, but small. There is
thus a resemblance between the anterior part of the tongue
in this animal and that in the Sirenians and some Ungulates
(**25**). When viewed from the side these papillæ are very
obtrusive features. The intermolar eminence is transversely
ridged. There is no trace of the foramen cæcum, sublingua,
plicæ fimbriatæ, or sulci on the ventral or dorsal surface; and
there are no frenal lamellæ. I was unable to cut into the
specimen examined to see if there is any lytta, as it is part of
the collection in the Museum of the Royal College of Surgeons.
Oppel (**14**) states that there is no lytta.

Poulton (**17**) has shown that the most anterior part of the
tongue is tactile and glandular, the middle part is mechanical in
function, and the intermolar eminence possesses the gustatory
organs and has glands. He, Oppel (**14**), and others have dealt
very fully with the histology of these structures, which are
of a primitive type; it is useless to describe any facts now-
adays unless they are absolutely new or different from their
statements.

In the Ant-eaters the tongue has the same general form as in

the insectivorous Edentata, for it is really a glutinous prehensile organ.

The external characters of note are:—

1. The anterior three quarters of the tongue is vermiform.
2. The posterior quarter is square.
3. There is a marked hollowing out of the anterior third, making a dorsal groove whose floor has a median row of spines.

Text-figure 44.
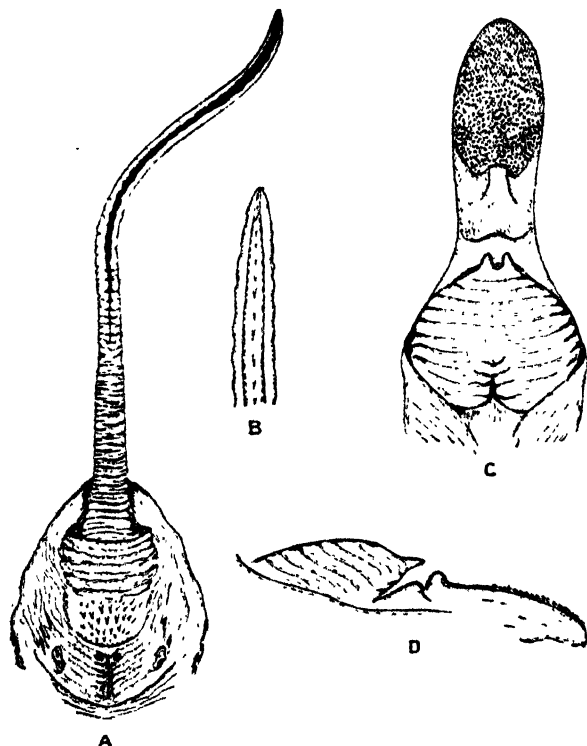
The tongues of the Monotremata. A: *Echidna*; B: gutter on front of tongue of *Echidna* opened to show spines; C. D: dorsum and side view of tongue of *Ornithorhynchus*

4. There is a median ventral groove anteriorly.
5. There is a median dorsal groove on the posterior part.
6. The dorsum on the posterior part has a patch of spines.
7. There are two sunken vallate papillæ.
8. The lateral organs are well marked.
9. There are no traces of the foramen cæcum, plicæ fimbriatæ, sublingua, or frenal lamella.

There is no lytta.

The primitive characters of the gustatory organs and the various groups of spines distinguish the tongue from those in the insectivorous Edentata. The histology has been fully described by Oppel (14), who also has collected the observations of other anatomists.

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32. On the Intra-renal Course of the so-called " Renal Portal " Veins in some common Indian Birds. By BASANTA KUMAR DAS, M.Sc., Empress Victoria Research Scholar of the Allahabad University, Allahabad, U.P., India *.

(Text-figures 1–10.)

CONTENTS.

1. *Introductory.*

In the present paper my object has been to give an account of the construction of what is commonly termed the "Renal Portal" system, as found in a number of birds for the most part peculiar to India. As judged by references to the subject in available text-books, opinions differ as to whether the *renous* blood conveyed to the kidneys in birds by the renal afferent veins takes part in the kidney capillary circulation or not. Thus Parker, in his 'Course of Instruction in Zootomy' (1900, p. 234), states that "during its course through the kidney the ·renal portal' gives off several small afferent renal veins to the middle and posterior lobes, the anterior lobe being supplied by similar vessels springing from the anterior face of the femoral vein," and in consequence infers that the renal afferent vein breaks up in the kidney substance; and Thomson, in his 'Outlines of Zoology' (1906, p. 646), makes a similar remark: "A hint of a renal portal system is represented by small branches which the femorals give off to the kidneys."

On the other hand, Shipley and MacBride in their 'Zoology' (1915, p. 623) state that the "renal portal pours its blood into the inferior vena cava, not as in amphibia and reptiles through a system of capillaries, but directly by a single vessel channelled through the substance of the kidney," and similarly Sedgwick in

his 'Student's Text-book of Zoology' (vol. ii. 1905, p. 441) comes
to the conclusion that "the renal portal circulation appears to be
absent; all the blood from the hinder part of the body passes
either directly into the inferior vena cava or by the coccygeo-
mesenteric into the hepatic portal system." A similar difference
of opinion was current in the middle of the last century.   Thus
Owen writes in Todd's 'Cyclopædia of Anatomy and Physiology'
(vol. i. 1835–1836, article "Aves," p. 348): "A difference of
opinion, however, prevails as to the course of the blood in the
veins which pass from the lower end of the kidneys to the hypo-
gastric vein.   Jacobson considers that the venous blood is carried
into the kidneys by these veins for the purpose of affording the
material for the urinary secretion, analogous to the portal vein in
the liver; but Cuvier regards these veins as having the same
function as those which come from the upper ends of the
kidneys, and that they return the blood from the lower ends of
the kidneys to aid in the formation of the portal veins.   Nicolai
also *opposes* the doctrine of a venous circulation in the kidneys of
birds"; and in his own 'Comparative Anatomy and Physiology of
Vertebrates' (vol. ii. 1866, p. 228) Owen expresses his opinion
decidedly in the negative: "A certain retention of the oviparous
type in the apparent entry of veins into the lower ends of the
kidneys is shown, but *a reni-portal vein does not exist*; the con-
nection of the lower veins coming from the kidney with the
iliaco-mesenteric is of such a kind that the renal venous blood
may flow to the portal system of the liver when that system and
digestion are at work; or it may flow by the upper emulgent
veins to the inferior cava and so to the lungs, when respiration is
unusually active."

Since the "renal portal" veins of birds have not previously
been studied from the physiological standpoint, and assuming for
the present that the "renal portal" veins really do convey venous
blood to the kidney, the sole means of deciding whether or not
the "Renal Portal System" of birds is identical in construction
with that of the lower vertebrates (fishes, amphibians and
reptiles) is to ascertain whether the renal afferent vein "*capil-
larizes*" to any extent (or at least subdivides up into small
sinusoids) in the substance of the kidney, or whether it merely
traverses the kidney and opens with undiminished calibre into
the renal afferent vein or the femoral vein.   This limited line
of enquiry is the one I have pursued, and my results are con-
tained in the following pages.

2. *The Veins associated with the Kidneys and the Intra-renal
   Course of the "Renal Portal" Veins in the Pigeon* (Columba
   intermedia) *taken as a type.*

The only vein which can possibly be considered to give rise to
a "Renal Portal" system is that which is often termed the
"Renal Portal." As will be seen from text-fig. 1, A, the two

" renal portal " veins (R.A.V.) and the coccygeo-mesenteric (CM.) all arise from a common centre, into which also opens the small "caudal" vein (C) and the small median cloacal vein (M.C.V.)

Since both of these "renal portal" veins and the coccygeo-mesenteric are all large veins assumed to be carrying blood *away* from the common centre, it is evident that they must on this assumption be regarded merely as reservoirs of venous blood fed by the two small veins just mentioned. The coccygeo-mesenteric at its point of origin appears to be of slightly larger calibre than either of the renal afferent veins (Dr. Woodland informs me that in amphibia the anterior abdominal vein is also considerably larger than either of the two renal afferent veins in the Frog and Toad), and receives further contributions of blood by way of small factors from the cloaca, the rectum and the hinder end of the small intestine. It carries the blood dorsal to the rectum (in the mesorectum) and opens into one of the large factors of the hepatic portal vein. The coccygeo-mesenteric vein, therefore, is solely to be regarded as a division of the hepatic portal system of veins, since, although it is connected with the two renal afferent veins, it is commonly assumed that it receives no blood from them. The two renal afferent veins, as already stated, are, at their point of origin, slightly smaller in calibre than the coccygeo-mesenteric, but two or three millimetres from the point of origin each receives a fairly large internal iliac (In.Il.) vein and three small dorsal parietal veins conveying blood from the caudal and the sacral regions. After receiving these factors, each renal afferent vein pursues its way to the hind end of the kidney (receiving just before it enters, on its inner or anterior side, another small vein (D) returning blood also from the sacral region) which it penetrates and takes the course now to be described.

Before describing the course of each renal afferent vein through the kidney substance, we must pause to make comment on the apparently limited sources of blood available for filling the three large veins—the two renal afferents and the coccygeo-mesenteric— compared with the plentiful supply available for the two renal afferents and the anterior abdominal of amphibians and reptiles. Since we know that in the two latter groups the two renal afferent veins do break up into a system of sinusoids in the kidney substance—a process which must offer considerably increased resistance to the blood traversing the kidney,—and that these veins are individually smaller than either of the two large femoral veins supplying them, it would appear that the mere fact that, in the Pigeon and birds generally, the two renal afferent veins are very large as compared with the veins which supply them with blood, may imply by itself that the avian " renal portal " veins do not branch in the kidney substance, but simply traverse it as reservoirs freely continuous with the post-caval vein. As we have seen, Owen, following Cuvier in part, concluded from this very different construction of the renal afferent

Text-figure 1.

A.

B.
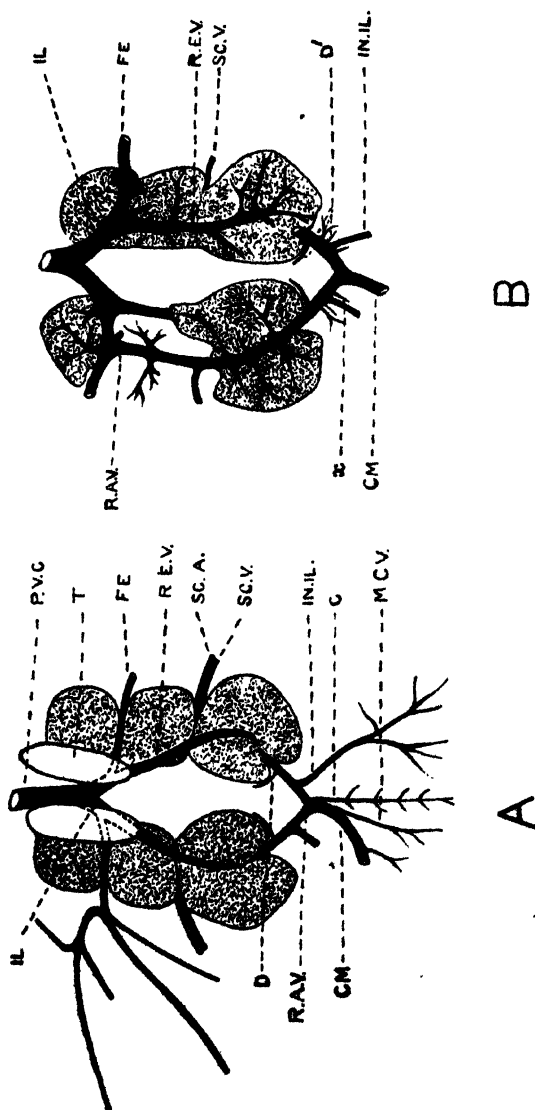
Diagram showing the veins of the kidney in the Pigeon (*Columba intermedia*).

A. (× 1·5). Ventral aspect. C, caudal vein; CM., coccygeo-mesenteric vein; D, small vein from the sacral region opening into the renal afferent vein; Fɪ, femoral vein; Iɪ., iliac vein; Iɴ.Iʟ., internal iliac vein; M.C.V., median cloacal vein; P.V.C., posterior vena cava; R.A.V., renal afferent vein; R.E.V., renal efferent vein; Sc.A., sciatic artery; Sc.V., sciatic vein; T, testis.

B. (× 1·5). The course of the renal afferent and renal efferent veins inside the substance of the kidney, as seen after dissection from the dorsal side. Letters as in A; in addition, D', small veins opening into the renal afferent from the sacral region; x, small vein from the proximal end of the caudal region.

veins in birds (compared with those of amphibia and reptiles) that the current of blood in the renal afferent veins of birds may not always be in an *anterior* direction, but that not infrequently it may flów *posteriorly*—*i.e.*, away from the kidneys and, with that of the internal iliacs and other factors, into the coccygeo-mesenteric vein; and in view of the small size of the caudal and the median cloacal veins, this idea does not appear to be improbable. Judging, however, from the direction of the currents observed in the perfusion experiment on the Duck, this view of Owen cannot be maintained, nor is it probable on grounds of comparative anatomy alone. To continue the description of the course of the " renal portal " veins anteriorly : Each "renal portal" vein on entering the kidney becomes deeply embedded in the posterior lobe, and soon comes to be dorsal to the renal efferent vein (R.E.V., text-fig. 1, B and text-fig. 2, C and D) and later crosses it, moving with a slight curve, convex to the outer edge of the kidney. While traversing the posterior lobe the " renal portal " vein receives seven main factors from its substance, and between the posterior and the middle lobe of the kidney it receives the large sciatic vein (S.C.V.), bringing blood from the proximal end of the thigh.

In the middle lobe the course of the renal afferent vein is more or less straight and uniform. From this region of the kidney it receives two important factors which open into it from opposite sides, and at the anterior limit of the middle lobe it opens into the large femoral vein (FE., text-fig. 1, B and text-fig. 2, M). There is also a small additional factor bringing blood from the substance of the middle lobe, which opens dorsally into the point of union of the femoral and the renal afferent veins. After opening into the femoral the renal afferent vein ceases to exist as such. Each renal afferent vein in its course through the kidney substance *postero-anteriorly distinctly increases in calibre*. Thus in one pigeon examined, the internal circumference of the *right* renal afferent vein posteriorly (where it first entered the substance of the posterior lobe of the kidney) was 2 61 mm , giving an area in transverse section of ·543 sq. mm. (see technique for methods), while *anteriorly* (immediately previous to its junction with the femoral vein) the internal circumference was 3·18 mm., giving an area in transverse section of ·807 sq. mm. ; the internal circumference of the *left* renal afferent vein *posteriorly* was 3·32 mm., giving an area in transverse section of ·908 sq. mm.; while *anteriorly* it was 3·5 mm., giving an area in transverse section of ·976 sq. mm. (*cf.* measurements of the renal afferent veins of the Duck given in the description of the type). This is part of the available evidence in favour of the view that the blood in the renal afferent vein flows *forwards* and *not* posteriorly, as has been supposed, and of the contention that the renal afferent vein does not give off *effluent* branches into the kidney substance.

Text-figure 2.
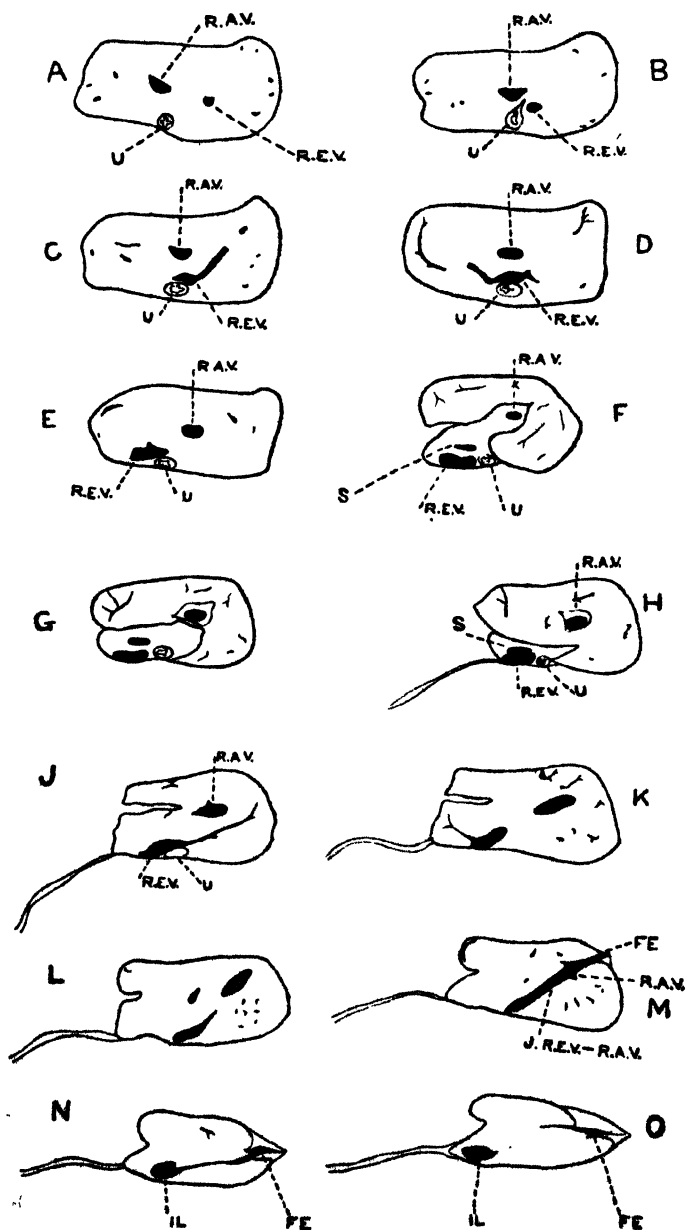
The veins of the Pigeon's kidney as seen in serial hand-sections. (× 2·5.)

It may not be out of place here to make some general remarks on the renal efferent and the femoral veins. Each of the two renal efferent veins originates in the substance of the posterior lobe of the kidney by the union of a number of principal factors (text-fig. 1, B). Each runs close to the ventral side of the kidney, at first a little apart from and slightly external to the ureter (text-fig. 2, B), but later it crosses the ureter dorsally, and comes to be situated towards the inner side of the ureter (text-fig. 2, C–J). The efferent vein is clearly visible on the ventral side of the kidney, especially when it is full of blood (text-fig. 1, A). Anteriorly each renal efferent vein pursues throughout its entire length a more or less straight course, approaching the inner side of the kidney the more anteriorly it is situated. In the middle lobe of the kidney each receives two or more additional factors. Anteriorly each renal-efferent unites with the femoral vein to form the iliac vein (IL., text-figs. 1, A and B; 2, M, N, and O), and into the latter also opens a small factor which brings blood from the anterior lobe of the kidney : the two iliac veins shortly afterwards unite to form the posterior vena cava (P.V.C., text-fig. 1, A and B).

The femoral is quite a big vein, and is formed by the combination of three main factors (text-fig. 1, A)—the anterior factor is small, and brings blood from the proximal portion of the thigh ; the median factor is quite long, and is formed, as usual, by the union of the peroneal and tibial veins bringing blood from the foot and the leg respectively, while, passing up the thigh, it receives some five or six additional factors draining blood from that region ; the posterior factor is a very fine long vessel running along the pubic bone, and brings blood from the cloacal and the pelvic regions. Close to its entrance into the iliac vein the femoral receives a factor which brings blood from the anterior lobe of the kidney (text-fig. 1, B).

3. *Conditions in other types of Indian Birds.*

Though in its main features the " Renal Portal " system of the other Indian birds which I have examined is of the same type as that just described for the Pigeon, *i. e.*, the blood conveyed to the kidneys by the renal afferent vein evidently does not pass through a sinusoidal system, yet there exists some variations relating to the disposition of the veins which are perhaps worthy

In A, the renal efferent vein (R.E.V.) situated towards the outer side, and the renal afferent vein (R.A.V.) to the dorsal and slightly to the inner side of the ureter. In D, the renal afferent vein lying quite dorsal to the renal efferent vein, and in E, the renal efferent crosses the ureter dorsally and comes to lie on its inner side. M, a slightly oblique section through the hinder end of the anterior lobe of the kidney at the level of the union of the femoral and the renal afferent veins (J.R.E.V.–R.A.V.). Letters as in text-fig. 1, A ; in addition, S, a small factor of the femoral vein ; U, ureter.

Text-figure 3.

A   B   C
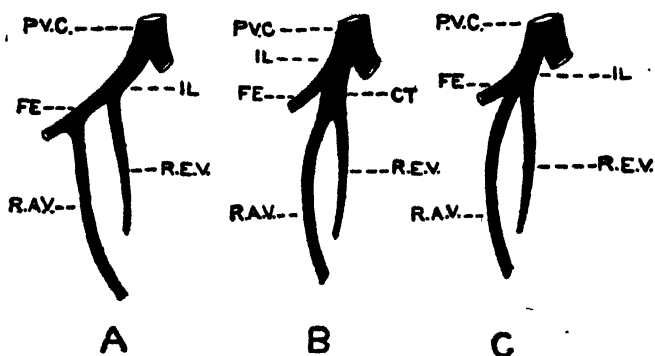
Diagrammatic plan of the three types of vein-arrangement as seen in
a number of Indian birds.

A, the first or Pigeon type; B, the second type, as seen in the Duck and the
Common Bulbul; C, the third type, as seen in the Parrot, the Vulture and
the Kite; common trunk, CT., formed by the direct union of the renal
afferent and the renal efferent veins.

Text-figure 4.
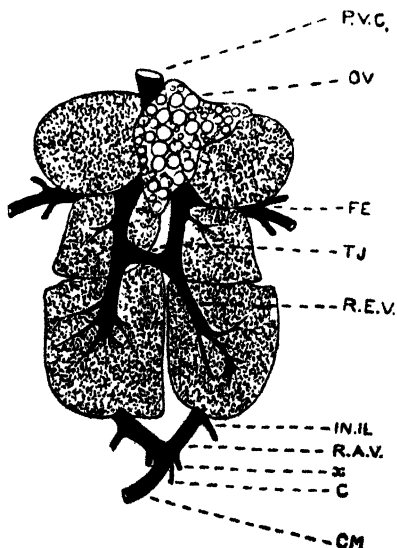
Diagram of the ventral aspect of the kidneys of Woodpecker (*Picus macei*, ♀, ×3),
showing the transverse junction (TJ.) between the two renal efferent veins.

Letters as in text-fig. 1, A and B; in addition, Ov., ovary;
only the important veins shown.

of record. Three main types of vein-arrangement can be recognized (text-fig. 3, A, B and C) :—

1. The first type is that described for the Pigeon, *i. e.*, each renal afferent vein opens into the femoral vein, and the latter then unites with the renal efferent vein to form the iliac vein; thus the renal afferent vein does not unite directly with the renal efferent vein (text-figs. 1, B and 3, A).

Text-figure 5.
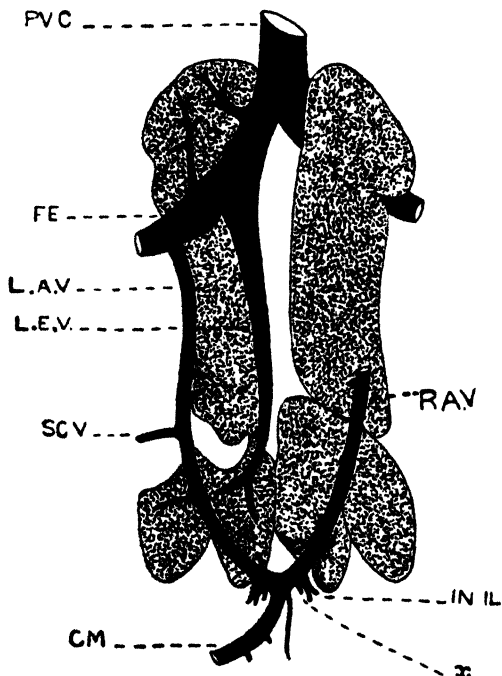
Diagram showing the course of the renal afferent vein (L.A.V.) of the Sarus Crane (*Grus antigone*) lying in a groove on the dorsal side of the kidney (× 1). Much of the substance of the left kidney dissected out, and the right renal afferent vein (R.A.V.) cut away about half of its length. Only the principal veins shown.

Letters as in text-fig. 1, A and B; in addition, L.A.V., left renal afferent vein ; L.E.V., left renal efferent vein.

This type is found among many of the birds I examined, *e. g.*, the Domesticated Fowl (*Gallus*), the Magpie (*Dendrocitta rufa*), the Woodpecker (*Picus macei*, in which the two renal efferent veins are connected transversely by a horizontal junction, text-fig. 4, TJ), the Falcon (*Falco peregrinus*), the Green Barbet (*Cyanops viridis*), the Spotted Owlet (*Athene brama*), the Blue

Text-figure 6.
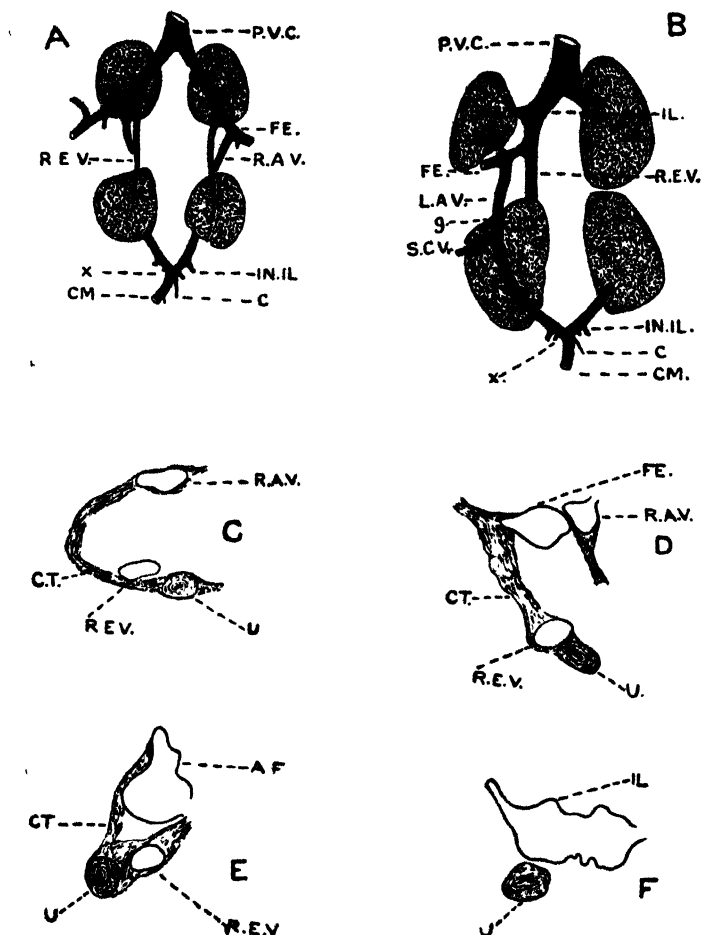
Diagrams showing the principal veins both from the ventral (A) and the dorsal (B) aspects, and also in serial hand-sections (C-F, × 6) of the kidneys of the Grey Hornbill (*Ocyceros griseus*). L.A.V., left renal afferent vein.

In A (× ⅔), the kidneys consist of two lobes, quite separate from each other, and the renal afferent vein (R.A.V.) is indicated to have crossed the renal efferent vein (R.E.V.) dorsally; the renal afferent vein running along a definite groove (B, *g*; × 1·5) on the dorsal surface of the posterior lobe of the kidney; C, hand-section of the kidney at the level in front of the posterior lobe; D, the renal afferent vein coming close to the femoral vein; E, the opening of the renal afferent vein into the femoral vein; F, the formation of the iliac vein.

Letters as in text-fig. 1, A and B; in addition, A F, the union of the renal afferent vein with the femoral vein; CT, the connective tissue membrane.

Jay (*Coracias indicus*), the Common Myna (*Acridotheres tristis*), and the Cuckoo (*Eudynamis orientalis*).

In the Sarus Crane * (*Grus antigone*; five specimens of which I have examined ; text-fig. 5), the Stilt† (*Himantopus candidus* ; three specimens examined), the Kite (*Haliaster indus* ; three specimens examined), and the Falcon (three specimens examined) it may be mentioned that the renal afferent vein runs *superficially* over the dorsal side of the kidney in a groove instead of lying in the interior of the kidney substance as in the examples already mentioned. This is also the case in the Grey Hornbill (*Ocyceros*

Text-figure 7.
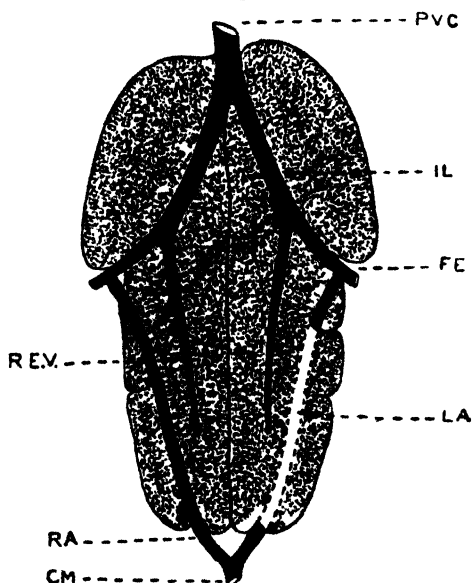
Semi-diagrammatic view of the ventral aspect of the kidneys of the Pond-Heron (*Ardea leucoptera*), × 3, showing the disposition of the right (RA) and the left (LA) renal afferent veins.

Letters as in text-fig. 1, A.

griseus; eight specimens examined), the kidney of which is also distinguished from that of other birds in general by the fact that it consists of two lobes only (text-fig. 6, A and B), the anterior and the posterior, the middle lobe being absent. The anterior and the posterior lobes are quite separate from each other, being about 11 mm. apart.

A peculiar arrangement (text-fig. 7) is also met with in the

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* This Crane possessed legs about 2 feet long, and the kidneys, though large, were not differentiated into three distinct lobes.

† The Stilt I examined had legs about 3 feet long.

Pond Heron (six specimens examined). In this type the disposition of the veins differs in the right and left kidneys. The *right* renal afferent vein (R.A.) does not become embedded in the kidney substance, but from the point at which it comes into contact with the kidney it lies more or less *superficially* on the *ventral* surface of the kidney, and passing anteriorly parallel and close to the renal efferent vein opens into the femoral vein; the *left* one (L.A.), on the other hand, becomes *deeply* embedded for some distance in the posterior lobe lying towards the dorsal side, but towards the anterior end of the posterior lobe it descends towards the *ventral* side of the middle lobe, where it can be well seen from the outer ventral aspect.

Text-figure 8.
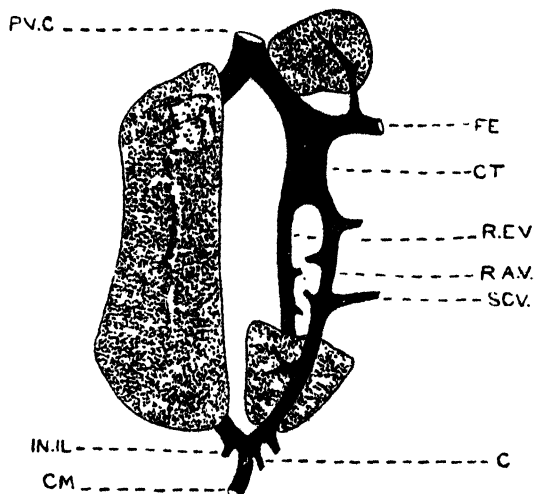
Semi-diagrammatic view of the arrangements of the renal afferent and the renal efferent veins of the Common Bulbul (*Pycnonotus pygæus*) from the dorsal side, ×4.

Much of the substance of the right kidney dissected out, and only the principal veins shown.

Letters as in text-figs. 1, A and 3, B.

2. In the second type (text-fig. 3, B) the renal afferent vein unites directly with the renal efferent vein to form a common trunk at about the level of the anterior end of the middle lobe of the kidney, and the common trunk unites anteriorly with the femoral vein to form the iliac vein.

This type of vein-arrangement is met with in the Domesticated Duck (of the genus *Anas*) and the Bulbul (*Pycnonotus pygæus*; two specimens examined; text-fig. 8). In the former type I repeated the measurements made on the Pigeon—that is,

I carefully measured the calibres of the two renal afferent veins posteriorly (at the level of their points of entrance into the kidneys) and anteriorly (just previous to their union with the renal efferent veins). The internal circumference of the right renal afferent vein as measured posteriorly was 7·3 mm., thus giving an area in transverse section of 4·521 sq. mm.; while anteriorly it was 6·8 mm., thus giving an area in transverse section of 3·662 sq. mm.; the internal circumference of the left renal afferent vein posteriorly was found to be 6·7 mm., thus giving an area in transverse section of 3·600 sq. mm.; while anteriorly it measured 7·2 mm., thus giving an area in transverse

Text-figure 9.
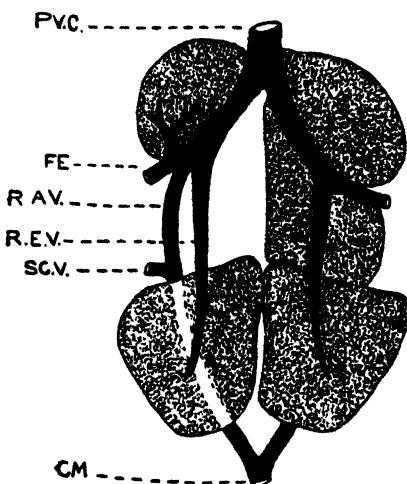
Semi-diagrammatic view of the ventral aspect of the kidneys of the Parrot (*Palæornis alexandri*), × 3, showing the union of the renal afferent, the renal efferent and the femoral veins at one point. Much of the right kidney has been dissected out, and only the course of the chief veins shown.

Letters as in text-fig. 1, A.

section of 4·30 sq. mm. Thus the two veins are apparently unequal in calibre throughout their course in the kidney. The thickness of the vessels could not be measured as their walls were too thin, and though the inner lining layer was quite definite, yet the outer wall was too indefinite to give any accuracy to the measurement.

3. The third type consists of the union of all the three principal veins at one point—the renal afferent, the renal efferent and the femoral (text-fig. 3, C).

This type of arrangement is found in the Parrot (*Palæornis alexandri*; five specimens examined; text-fig. 9), the Vulture

(*Gyps bengalensis*; three specimens examined), and the Kite (*Haliaster indus*; three specimens examined).

In the majority of birds examined I noticed that the point of junction of the femoral vein with the iliac vein is clearly visible at the anterior end of the middle lobe of the kidney from its ventral side ; but in some cases, however, *e. g.*, the Common Myna (*Acridotheres tristis*), the "Seven Sisters" (*Crateropus canorus*),

Text-figure 10.
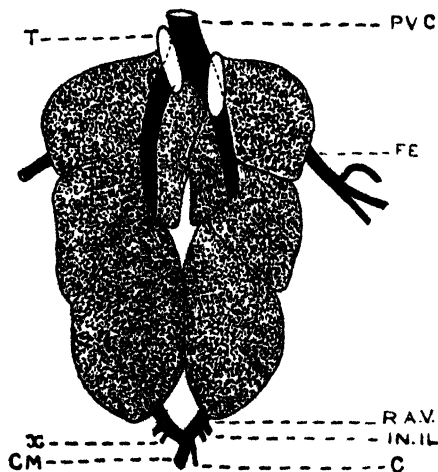
Diagram showing the course of the femoral vein just before it is embedded in the substance of the anterior lobe of the kidney of the Stilt (*Himantopus candidus*) from the ventral aspect, × 1.

Letters as in text-fig. 1, A and B.

the Spotted Kingfisher (*Ceryle rudis*), the Indian Hoopoe (*Upupa nigripennis*), the Stilt (*Himantopus candidus*; text-fig. 10), and the Woodpecker (*Picus mace*; text-fig. 4), the femoral becomes embedded within the substance of the kidney as soon as it comes in contact with it, and thus the point of union is situated inside the kidney.

4. *Some general remarks.*

From certain experimental results (which will be published in another journal) of a physiological character I observed that the current of the dye (and hence that of the blood) was anterior in the renal afferent vein, but there was some tinging of the kidney substance in places which was due to a very slow physical process of simple diffusion, and would thus present an erroneous impression with regard to the non-capillarization of the renal afferent vein. But the conclusion that the renal afferent vein does not capillarize is also strengthened by calibre measurements of veins.

The diameter of the renal afferent vein (right and left) at the anterior end of the kidney (in Duck and Pigeon examined) is greater than at the posterior end, which implies that it must have been fed by venous tributaries during its passage through the kidney substance, and that it does not give out branches which would ultimately capillarize, because if the latter condition exists, it would be quite reasonable to expect the diameter of the vein at the anterior part of the kidney to have become decidedly smaller as compared with that at the posterior end ; but this is exactly contrary to the observed facts—it actually gains in calibre from behind forwards as it gradually proceeds towards the anterior end (*cf.* measurements given in the text).   Thus it follows that the renal afferent vein (the so-called "Renal Portal") during its course through the kidney does not capillarize (as in fishes, amphibians and reptiles), but it receives the renal venous blood through a system of channels (really renal veins) which is then poured into the posterior vena cava.   The presence of numerous small renal veins (*i. e.*, the venous channels just referred to), in addition to the large renal afferent vein, which pour their blood into the renal afferent vein (this vessel presumably being nothing more than a big reservoir of blood) is probably correlated with the increased functional activities in Aves.

Another point of great interest observed in the course of experiments was that the urine of birds was not liquid, but semisolid.   Since, when the aorta was perfused in just freshly-killed birds with a very dilute saline solution, the first lot of urine secreted was still milky in appearance, and, in fact, strongly resembled the natural urine secreted previous to the experiment, it would appear probable that the kidney itself secretes the semisolid urine characteristic of birds, and that the statement, quoted by Cushny[*] (from Sharpe), that the urine of birds as formed by the kidneys is liquid, like that of a mammal, while travelling down the ureters, and only assumes its semi-solid character by subsequent absorption of water in the cloaca, is erroneous.

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[*] Cushny (**2**, p. 53) states that "A more cogent argument is the absorption of urine itself in birds ; in these the urine passes down the ureter as an abundant and generally clear fluid, but in the bowel the water is almost absorbed, leaving a thick paste of urate (Sharpe, 1912)." In order to verify Cushny's remarks, I examined half-a-dozen of Indian birds (viz., Pigeon, Duck, Crow, Myna and Parrot), and I found that, in each and every one of them, the ureter from the very beginning was full of semi-solid cream-coloured (or slightly yellowish) urine. I never found any visible trace of watery fluid under natural conditions in any part of the ureter, the wall of which was sufficiently thin as to allow the semi-solid matter to be seen along its whole length.

The semi-solid urine passes down the ureter by a peculiar peristaltic movement of the muscular walls, and on reaching the cloaca it is voided along with the fæcal matters. It may be said that the kidneys, even long after they were perfused with the saline mixture, secreted highly milky urine, which gradually took the form of a watery fluid when all the solid urates were got rid of during perfusion. This conclusively proves (exactly similar features being observed in several other dissected specimens) that in birds the urine is always and from the very start solid, and not watery as in other animals, and this fact is probably correlated with the greater activity as compared with other animals, and hence the necessity for the conservation of water (circulating in the blood) by the renal cells.

5. *Summary and Conclusions.*

The facts recorded above may be summarized as follows :—

1. In their essential features all birds possess the same type of arrangement of veins as found in the Pigeon—*i. e.*, the blood has a direct communication with the posterior vena cava.

2. The mere fact of the large size of the two renal afferent veins and their comparatively meagre blood-supply (compared with amphibians and reptiles, where the renal afferent vein is plentifully fed by the large femoral vein and the sciatic vein) goes to show that there cannot be any " Renal Portal System " in birds.

3. The current of blood is always *anterior* in the renal afferent vein, and never in the reverse direction.

4. Each renal afferent vein communicates with the post-caval vein with undiminished calibre, and does not break up into sinusoids or capillaries in the substance of the kidney.

5. The kidneys of birds secrete semi-solid urine, and there is no absorption of water in the cloaca.

Lastly, I wish to express my most sincere thanks to Dr. W. N. F. Woodland, D.Sc., for his kind criticisms, preliminary advice and encouragement throughout the work. I must also acknowledge my indebtedness to him for kindly reading through the manuscript. To Professor MacBride it is my most pleasant duty to offer my best thanks for his many invaluable suggestions and for communicating the paper for publication.

6. *Technique and Material.*

A. The birds were opened out carefully from the ventral side behind the keel, and all the veins in connection with the kidney were ligatured. The kidneys were then removed, fixed and preserved in 6 % formalin for a week. In some cases, however, the birds were simply opened out, and put in the formalin without any ligature of the veins. The course of the principal veins has been ascertained carefully under the dissecting microscope. The whole mass of the kidney was imbedded in wax, and serial hand-sections, as thin as possible, were taken. These sections were not stained, as the principal veins in question being full of blood rendered the series easily traceable.

B. For the calibre-measurement of the renal afferent veins a Duck and a Pigeon were opened out from the ventral side without injuring any of the veins of the kidneys, and the whole bird preserved in formalin for a week. The kidneys were carefully dissected out, and a short length of the renal afferent vein both anteriorly and posteriorly from each of the kidneys was cut off, and stained in bulk with borax carmine for two days. The vessels were then imbedded in wax, and were treated exactly alike all the time. Several sections of the Pigeon 10μ thick

and those of the Duck 18μ thick were mounted on a fairly thick medium of Mayer's albumen, and then stained on the slide with picro-indigo carmine for about 5 minutes. They were washed very quickly with absolute alcohol (prolonged washing with the absolute alcohol will remove almost all the picro-indigo carmine stain); after clearing in xylol they were mounted in Canada balsam. Best sections of the series from the anterior and the posterior portions of each renal afferent vein of the Pigeon and the Duck were selected, and their internal circumference was drawn with the camera lucida on the Bristol board under a magnification of about 171 diameters for the Pigeon and about 76·7 diameters for the Duck. The internal circumference was measured by means of a string passed exactly round the circumference, and the areas were then calculated and compared.

A rough estimate of the areas of the vessels so drawn was also made by cutting away the Bristol board just along the line of the internal circumference, and then weighing the strips of paper, but owing to re-entrant curves (the vessels not being properly full of blood) this method was of little value.

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33. On a New Land Nemertean from New South Wales (*Geonemertes hillii*, sp. n.).   By MARY L. HETT, B.Sc., F.Z.S.

(Text-figures 15–22.)

The following observations were made on specimens of *Geonemertes* collected in N. S. Wales by Professor J. P. Hill, who kindly placed his material at my disposal. I also wish to express my thanks to Professor Dendy for the gift of a specimen of *Geonemertes australiensis*, which was studied for purposes of comparison.

The following notes on the occurrence and external features of the living animal were made by Prof. Hill at the time of capture :—

"*Geonemertes* from the scrub about a mile down the Barrington River (N. S. Wales). Not uncommon under logs if the soil is good. It readily attracts attention owing to the bright red bands which are exceedingly conspicuous. When touched, it at once shoots out a long proboscis of a pinkish colour and begins to move off rapidly. The ejection of the proboscis, and the resulting movement of the organism are so sudden as to be startling. It progresses in a rapid gliding manner, apparently effected partly by wave-like movements of the proboscis, while finally, during introversion of the latter, the body is drawn forwards, the sticky surface of the proboscis adhering to the sub-stratum."

"*Colours.* Purple-brown dorsally, with two bright red lateral bands extending over the anterior two-thirds of the body. Posterior end dark, almost black in some. It tapers to a blunt point. Ventral surface a light mottled brown. Proboscis of great length, of a light pinkish colour."

There were five specimens varying from 23 mm. to 45 mm. in length, and from 1·5 mm. to 5 mm. in width at the broadest part, about the middle of the body. One of these, 27 mm. in length, was a male; two were females (25 mm. and 45 mm. long respectively); the remaining two (36 mm. and 38 mm. long) were not sectioned, but from their size were probably females.

The ground colour of the spirit specimens was a lightish brown, with the dorsal surface of a darker purplish brown, the ventral surface mottled. A light-coloured band on each side no doubt represented the red bands noted above. Eyes were not visible (text-fig. 15).

Sections were cut at $4\,\mu$, $7\,\mu$, and $10\,\mu$. Several stains were employed to demonstrate their structure. The most successful were:

(1) Ehrlich's hæmatoxylin, with eosin as a counter stain.

(2) Iron hæmatoxylin.

Iron hæmatoxylin showed the blood-vessels more clearly and stained some of the glandular secretions deeply, but the first-named method was the better for general purposes.

Prof. Dendy's specimen of *Geonemertes australiensis* was sectioned at $7\,\mu$ and treated with Ehrlich's hæmatoxylin and eosin.

Text-figure 15.

Geonemertes hillii with proboscis extruded.
(Drawn from spirit specimen.)

GEONEMERTES HILLII, sp. n.

Length: 23 mm. to 45 mm. Colour: purple-brown dorsally, ventral surface light mottled brown; two conspicuous bright red lateral bands on the anterior third of the body. Two paired groups of eyes, the total number of eyes being about 40. No cephalic gland. The vascular system with an extensive network of branching vessels. Nephridia exceedingly numerous and unconnected by longitudinal canals.

Habitat: New South Wales.

Geonemertes hillii bears a close resemblance to *G. australiensis* Dendy, not only in general anatomy, but also in size, habitat,

and the presence of numerous small eyes. It differs from it, however, in :—(1) apparent absence of the cephalic gland ; (2) number and arrangement of eyes; (3) details of vascular and excretory systems; (4) coloration.

CEPHALIC GLAND.

The absence of the cephalic gland is a very noteworthy feature, since it is conspicuous in almost all the other members of the genus. The only other species of *Geonemertes* in which the cephalic gland is stated to be absent is *G. dendyi* Dakin (1) from W. Australia, which resembles *G. australiensis* in many respects, but is distinguishable not only by the absence of the cephalic gland, but also by its smaller size, by its coloration, and by the smaller number of eyes.

The cephalic gland in *Geonemertes* consists of a mass of large irregular cells with granular cytoplasm and small nuclei, lying mainly dorsal to the brain, and in some cases extending backwards as far as the stomach. It usually opens to the exterior by a pair of ducts, but there may be a number of smaller ducts opening independently on the sides of the head. In *G. australiensis*, Prof. Dendy remarks (2): " the appearance of my sections leads me to believe that the secretion is passed out through extemporised channels on the back and sides of the head." This was certainly the case in my own sections of *G. australiensis*, where the secretion could be clearly seen passing to the exterior in the manner described. In this species the gland stains deeply with hæmatoxylin. Prof. Dendy states that it is only slightly affected by borax carmine; I found the same with regard to eosin.

In addition to the cephalic gland, there are frequently present below the muscle layers of the body-wall in the head region, a number of gland-cells of a different structure, and with different staining properties, called by Dendy "dorsal glands." These, as pointed out by Coe (3), are specialised integumentary glands which have sunk below the surface. In *G. australiensis* they are most abundant in the dorsal region just behind the head, but are found in small numbers throughout the body.

Schröder (5) has thrown doubt on the glandular nature of the so-called "dorsal glands" in this species, and suggests that they may prove to be sections of the terminal cells of nephridia. This, however, is not the case. As shown below, they are entirely different in structure and appearance from the nephridia, and contain a mass of granular secretion. Moreover, they vary in size from about 12 μ–24 μ in length and from 8 μ–12 μ in breadth, whereas the terminal cells of nephridia are much smaller.

In *G. hillii* the cephalic gland could not be detected in any of the sections, but the above-mentioned integumentary glands were

largely developed (text-fig. 16). Failure to demonstrate the
cephalic gland was not, I think, due to anything in the fixation
of the material, since the sections otherwise stained extremely
well with hæmatoxylin; nor to peculiar staining properties of
the gland, since in sections of *G. australiensis*, similarly stained
for comparison, the cephalic gland was very conspicuous. As
described by Prof. Dendy (*l. c.*), it formed a mass of deeply-
staining cells dorsal to the brain. I also found a smaller mass
of similar gland-cells on the ventral side of the body in this
region.

The "dorsal glands" in *G. hillii* extend from the anterior
extremity throughout the greater part of the body, though they
become few and scattered towards the posterior end. As is

Text-figure 16.
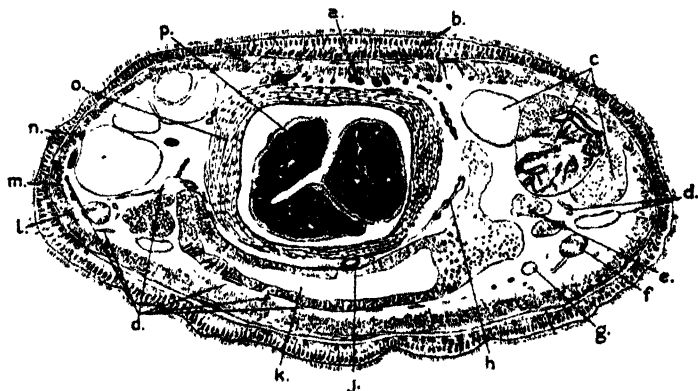
Transverse section of ♂ through the intestinal region, × 45.

a, "Dorsal glands"; *b*, epithelium; *c*, testes; *d*, sections of blood-vessels; *e*, diver-
ticulum of intestine; *f*, lateral nerve cord; *g*, lateral vessel; *h*, longitudinal
section of commissural vessel; *j*, dorsal vessel; *k*, intestine; *l*, longitudinal
muscles; *m*, circular muscles; *n*, section of nephridium; *o*, proboscis sheath;
p, proboscis.

usually the case, they are especially numerous in the head region,
and here particularly in the area dorsal to the brain, which is
occupied in other species by the cephalic gland. The cells are
much smaller than those of the cephalic gland, and in the earlier
stages are distinguishable by the fact that they stain deeply with
hæmatoxylin and possess a very distinct nucleus and nucleolus.
Later a granular secretion is formed inside the cell which pushes
the nucleus to one side. Eventually the cell consists of: (*a*) an
outer layer of cytoplasm which is extremely thin except at one
point where the nucleus is embedded: the cytoplasm and nucleus
stain deeply with hæmatoxylin; (*b*) an inner mass of granular
secretion which contains numerous little circular clear spaces,

looking like drops of an oily nature. This secretion, which stains deeply with eosin, passes to the exterior of the body through a fine duct which consists of flattened cells, and is not always easily recognizable (text-fig. 17). The cells may occur singly or grouped into clusters, and several cells may possess a common duct.

Text-figure 17.
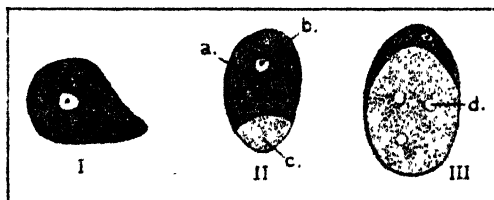
" Dorsal gland " cells. × 800.

I. Early stage.　II. Commencing formation of secretion.
a, Cytoplasm ; *b*, nucleus and nucleolus ; *c*, secretion.
III. Late stage.　　*d*, Clear spaces in secretion.

Eyes.

The eyes were not visible externally in the preserved specimens, but sections showed two pairs of groups of eyes : an anterior dorso-lateral pair, and a posterior dorsal pair, each containing a number of small eyes varying somewhat in size. These were similar in structure to those of *G. australiensis*, but they appeared to be more numerous. Prof. Dendy (*l. c.*) counted about 20 on each side in *G. australiensis* : in my own sections of his species there were rather more, but they could not be counted with entire accuracy owing to the fact that some of them were obscured by the cephalic gland. In *G. hillii* all the eyes could be seen clearly, the cephalic gland being absent. There were about 40 on each side, 30 in the anterior group and 10 in the posterior group. The anterior group showed a further incipient division into : (*a*) a set of eyes dorso-lateral to the brain with the cups opening dorsally ; (*b*) a smaller set ventral to the brain, the cups opening more ventrally. The eyes of the posterior group were on the whole smaller and more flattened than those of the anterior group, and the two groups were separated by a definite space representing at least 160 μ. Prof. Dendy states that in *G. australiensis* there was merely an indication of division of the eyes into an anterior and a posterior group. In my sections of his species the two groups were only separated by one section representing 7 μ.

So that the eyes in *G. hillii* differ from those of *G. australiensis* in :—

1. Much more definite division into two groups on each side.
2. Probably greater number of individual eyes.

Vascular System.

The vascular system is remarkable, consisting of a dorsal vessel, a pair of lateral vessels, and a very extensive system of branching vessels forming an anastomosing network which extends throughout the entire length of the body (text-fig. 16).

Anteriorly there are a number of large irregular blood spaces in the head region, some of which are connected with the dorsal vessel, others with the general network. The dorsal vessel has the general relations described by Prof. Dendy in *G. austra-liensis* (*l. c.*). It runs backwards just above the gut from the œsophagus nearly to the anus, but pursues a somewhat sinuous course and is by no means constant in diameter. Anteriorly it terminates in a mass of cells which form a marked swelling, and project into the cavity of the proboscis sheath below the ventral commissure of the brain. In *G. australiensis* there were two such swellings, one on either side. The main portion of the dorsal vessel passed to one of these, while a smaller branch which was given off laterally from the main canal ran to the swelling on the opposite side. Schröder suggests (5) that Dendy may have been mistaken in describing a double termination for the dorsal vessel. I am, however, able to confirm Dendy's observation, since in my own sections of *G. australiensis* the two swellings are very obvious and the condition there is as originally described. In *G. hillii* also the main vessel bends laterally and terminates in a swelling on the right side, but I could not trace any branch on the left. I cannot be absolutely certain that none was present as two of the sections were slightly defective at that point, but, if it were, it must be very small. In any case the conditions suggest, as in *G. australiensis*, that the vessel was originally paired, at all events at the anterior end, since in the œsophageal region it does not run in the median line, but lies laterally, on the side corresponding to the terminal swelling. Posteriorly it divides into right and left branches just behind the muscular attachment of the proboscis, and becomes connected with the general anastomosis. I was unable to deter-mine with certainty whether there were commissures given off from the dorsal vessel anterior to the intestinal region, because the commissural vessels are small and the dorsal vessel is very irregular in shape. Some of the vessels of the general network run close to the dorsal vessel, but I could not trace any con-nection between them in this region. In the intestinal region, however, paired commissures arise at intervals from the dorsal vessel and encircle the gut, giving off numerous branches. These run between the intestinal diverticulæ, gonads, etc., and anastomose freely, uniting distally with an irregular series of circular vessels below the longitudinal muscles of the body-wall, and ultimately breaking up into smaller branches.

This network is connected with the lateral vessels throughout their entire length.

The pair of lateral vessels lie mesial to the nerve cords, but it is not always possible to trace their course, which is very irregular, and complicated by the fact that they frequently expand into thin-walled sinuses or contract to a very small compass.

All the vessels have an inner endothelial layer with projecting nuclei, outside which is a basement membrane. In all except

Text-figure 18.
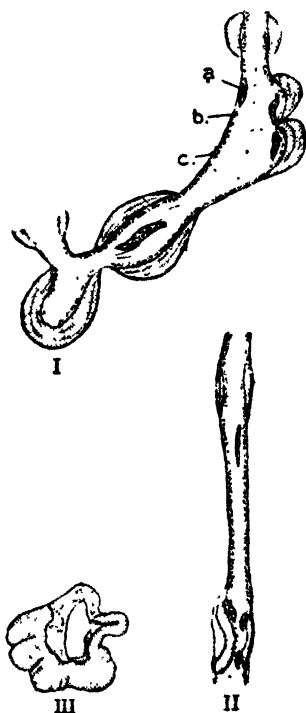
× c. 1300.

I. Longitudinal section of blood-vessel, showing "valve cells" projecting
    outwards: *a*, nucleus; *b*, endothelium; *c*, basement membrane.
II. Ditto, with "valve cells" projecting into cavity of blood-vessel.
III. Transverse section of blood-vessel through "valve cells."
    (Musculature is not shown in this figure nor in fig. 19.)

the lacunar spaces of the head there is an outer layer of circular muscles which in the dorsal vessel is relatively thick, but in the lateral vessels and the anastomosis relatively thin, and only to be seen clearly under high magnification. The dorsal vessel has, in addition, the usual outer sheath of vesicular cells which are, however, absent from the lateral vessels.

Except for the musculature the walls of the blood-vessels are stained to a greater or lesser extent by hæmatoxylin but not by eosin, and are recognizable in sections from this fact as well as from their structure. The muscle layer stains deeply with eosin and is therefore very noticeable in the dorsal vessel, but elsewhere it is not easy to make out. In all except the dorsal vessel there are also present at intervals in the basement membrane conspicuous elongated cells, more or less crescent-shaped in longitudinal section, as described by Böhmig (**4**) and others. In longitudinal section these cells appear to lie opposite to one another in pairs, but in transverse section they are seen to be somewhat irregular in arrangement, and in some cases they have a folded appearance. This is due sometimes to the branching of the vessel at this point, sometimes to the presence of three or more cells at one level (text-figs. 18 and 19). Occasionally, in longitudinal section, the cells show a striping parallel to their

Text-figure 19.
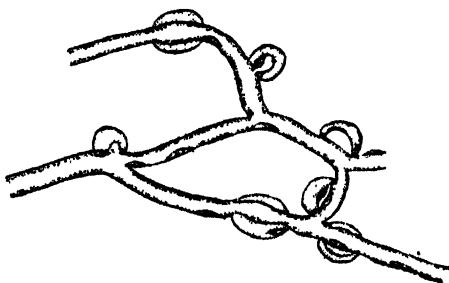
Portion of the vascular network, × 670.

length, and in some transverse sections there is also an indication of striation. Böhmig (*l. c.*) describes a similar condition in *G. chalicophora*, and states that this is due to a network of fine membranes in the cell substance, but in his specimens the striping was radial, while here it is longitudinal. The function of these cells is doubtful. Böhmig regarded them as possibly valves, regulating the flow of blood, but Coe (*l. c.*) considered that they were more probably secretory, and pointed out that they stained in a similar way to the other gland-cells present. This, however, was not the case in my sections: they stained rather lightly with hæmatoxylin and not at all with eosin, and the cytoplasm appeared more or less homogeneous.

From the above description it will be seen that the vascular system of *Geonemertes hillii* differs in several important respects, not only from that of a typical Metanemertean, but also from other species of the genus, especially with regard to the complicated system of branching vessels, and the presence of irregular lacunar blood spaces. The vascular network recalls the condition in

Malacobdella Blainville, but is much more extensive, being present throughout the entire body, from the extreme anterior to the extreme posterior end.

EXCRETORY SYSTEM.

The excretory system is very extensive. The nephridia bear a strong resemblance to those described by Schröder (5) for *G. palaensis* Semper. In that species there was an enormous number of nephridia opening to the surface at intervals all round the body*. In *G. hillii* they are equally numerous and appear to be unconnected by longitudinal canals. Each nephridium consists of :—(*a*) a short duct leading to the exterior; (*b*) a glandular portion; (*c*) branching end canals; (*d*) flame cells.

Text-figure 20.
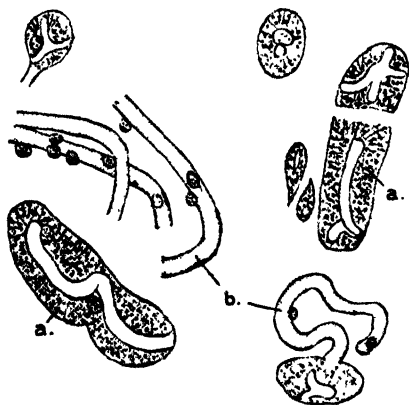
Portions of nephridial tubules, × 600.
a, Sections of glandular portion; *b*, portions of end canals.

The ducts are very fine and consist of flattened cells with relatively rather large nuclei. These ducts pass from the body parenchyma through the muscle layers, basement membrane, and epithelium to open to the surface by a minute pore. At its lower end each duct passes into a glandular portion which consists of cells whose outline is hard to distinguish. The lumen of the tubule is here intra-cellular, and the walls are thick. In many transverse sections the characteristic radial striation of the cytoplasm mentioned by several authors can be seen. From this portion are given off the end canals, which are frequently coiled and branch freely. They are of much smaller diameter than the glandular portion, and the projecting nuclei are conspicuous. The end canals terminate in very fine ducts leading to flame

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* Schröder estimated the number in one individual at something like 35,000.

cells, several of which are connected with one end canal. The flame cells, which are long and slender, measure about 8μ in length and about 1.5μ in breadth. A single nucleus is embedded in the cytoplasm at the tip of the cell, from which a long tuft of cilia passes into the lumen (text-fig. 20 A).

The nephridia are found the whole way round the body throughout its entire length, though they decrease in number towards the posterior end. They are exceedingly numerous, sometimes as many as 40 or 50 being present in one section. In the head region they are especially conspicuous, the whole of the parenchyma being filled with sections of nephridia and blood-vessels. Flame cells appear to be present throughout, but only in large numbers round the œsophagus: in the region of the intestine they are not easy to detect.

Text-figure 20 A.
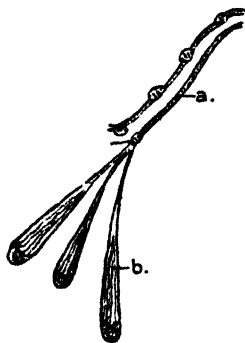
Flame cells, × 600.
a, End canal; b, flame cell.

The major part of each nephridium lies embedded in the parenchyma below the muscles of the body-wall; some of the glandular portion, however, and occasionally some of the end canals are found among the longitudinal muscles. The ducts, as before mentioned, traverse the muscle layers and epithelium.

The length of a nephridium varies considerably with its position: it is relatively short in those parts of the body where the internal organs are crowded together; where there is more space, e. g., in the ventral region mesial to the nerve cords, each section of the nephridium may be considerably lengthened. The nephridia run everywhere in close relation to the anastomosing blood-vessels; no connection could, however, be traced between the two systems.

The cytoplasm of the nephridia stains with eosin, but not very deeply. This serves to distinguish them on the one hand from the blood-vessels which are almost unaffected by eosin, and on the other hand from the integumental glands whose secretion

stains very much more deeply. The nuclei, both of the glandular portion and of the end-canals, are rounded and granular and stain lightly with hæmatoxylin.

On examining my sections of *G. australiensis*, I found similar tubules present there also, though they were not so numerous as in *G. hillii*, and Prof. Dendy, to whom I showed the slides, concurred in my opinion as to their excretory nature. I further believe the vascular system to be of the same type in both species, and that the branching network of fine vessels present in *G. australiensis* forms part of the circulatory and not of the

Text-figure 21.
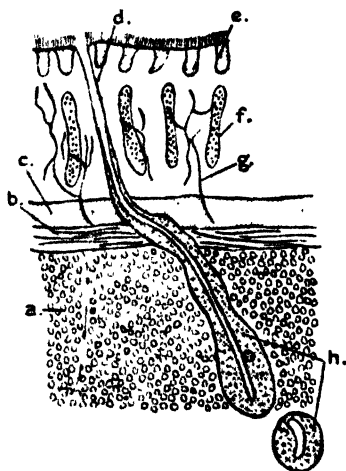
Nephridial duct, × c. 350.

a, Longitudinal muscles of body-wall; *b*, circular muscles of body-wall; *c*, basement membrane; *d*, duct of nephridium; *e*, epithelial cell; *f*, gland cell of epithelium; *g*, pigment cell; *h*, glandular portion of nephridium.

excretory apparatus. In my sections of *G. australiensis* these vessels had very large "valve cells." I am uncertain as to whether their peculiar appearance was due to difference in fixation, but they were more conspicuous than in *G. hillii*. These cells show great variation in shape, lying sometimes almost flat against the walls of the vessels, at others projecting into the cavity like a curved bow, or projecting in the opposite direction on the wall of the vessel (text-fig. 18). In *G. australiensis*, however, they project to a greater extent than in any of my sections of *G. hillii*.

PROBOSCIS.

There were 18 proboscis nerves and, in the only series in which they could be observed, there were 5 reserve stylet sacs.

REPRODUCTIVE SYSTEM.

Similar to that of *G. australiensis.* The sexes are separate. Copulation had taken place in the case of the two female specimens sectioned. The ova were found in all stages of development. The yolk is apparently derived from the cells of the follicle to which the ovum is at first connected by bridges of cells, but later the follicle is in contact with the ovum over the two-thirds of its surface. All the ovaries, except those in a very early stage, had ducts open to the exterior and containing sperms (text-fig. 22). Each duct consisted of : (*a*) a narrow channel passing through the epithelium and dilating slightly in the region of the basement membrane to form a kind of chamber, at which point the sperms were always found ; (*b*) an epithelial tube continuous with the ovary wall and traversing the muscle layers. It seems doubtful whether this channel can also serve as an oviduct, owing to its narrow dimensions and the large size of the ovum. On fixation of one of his specimens, Prof. Hill

Text-figure 22.
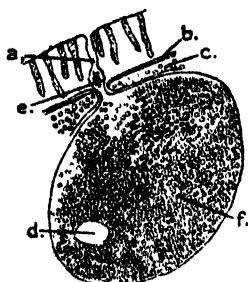
Ripe ovum, × c. 60.

a, Vaginal duct; *b*, circular muscles of body-wall; *c*, longitudinal muscles of body-wall; *d*, nucleus; *e*, sperms in vaginal duct; *f*, yolk.

noticed that an ovum was extruded through the dorsal body-wall, which was ruptured at this point, but he was unable to determine whether or no the rupture was caused by the reagent. The extruded egg was preserved, and on examination I found it to be nearly circular; it measured ·54 mm. in diameter, which is probably a little less than in the fresh condition. The vaginal canal does not appear to close again after fertilization, so that possibly the ovum may reach the exterior through this passage, enlarging the aperture by rupture of the surrounding tissues.

The male specimen contained sperms in all stages of development, and many of the ripe testes had ducts very similar in structure to the oviducts and containing sperms. These ducts did not appear to open to the exterior, except where the sperms were ripe. Unlike the condition described for *G. australiensis,* the developing sperms were enclosed in a capsule at a very early stage, it was thin but in most cases quite distinct.

The general agreement of the anatomy of Prof. Hill's specimens with that of *Geonemertes australiensis* (especially in regard to the unusual arrangement of the vascular and excretory systems) would have led me to consider them as belonging to the same species, in spite of differences in detail, had it not been for the absence of the cephalic gland in the former case. This remarkable feature, however, taken in conjunction with the smaller differences mentioned above, appears to be of sufficient importance to justify the creation of a new species, for which I have proposed the name *Geonemertes hillii*. There is no doubt, however, that the two species are closely related and possibly should be grouped apart from other species of the genus together with *G. dendyi* Dakin. In his account of the latter, Prof. Dakin describes four groups of eyes, the total number of eyes present being about 16, and he notes the absence of a cephalic gland. He makes no specific reference to the vascular or excretory systems, but states that the anatomy of *G. dendyi* does not differ in any important respect from that of *G. australiensis*. Thus all three forms are characterized by the presence of numerous small eyes arranged in paired groups, while *G. hillii* and *G. australiensis*, possibly also *G. dendyi*, agree in possession of a branched vascular system and a large number of small nephridia. *G. hillii* and *G. dendyi* further resemble each other, and differ from *G. australiensis*, in the absence of a cephalic gland. *G. dendyi* differs from *G. hillii* and *G. australiensis* in size, coloration, locality, and number of eyes.

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34. Some Remarks on the Pelvic Bones of Parrots. By E. MAUD KNOBEL, F.Z.S.

(Text-figure 1.)

The question of sexing birds whose plumage is the same in both male and female has always been a problem. This especially applies to Parrots, though those coming from India and Australia in most cases have some distinguishing mark to tell the males from the females; those from Africa, such as the Grey, the Senegal, and Meyer's, and the forty-two different species of Amazons from Mexico and South America have the same plumage in both sexes.

Many suggestions have been put forward for determining the sex in Parrots, such as the shape of the beak, whether long and narrow, or thick and broad, the colour of the eye, the shape of the head, whether round or flat and so on, but none of these has proved satisfactory.

For many years I have kept Parrots, more than perhaps most people, having had forty-three. Out of these twenty-five have been Amazon Parrots, of which I have had ten different species.

I have always been able to sex my own birds by feeling the pelvic bones. In the male bird the pelvic bones lie so close together that they feel as if they actually touched, but in the female they are wider apart. In a young female they may be very close together though they never actually touch, but one may be deceived and one has to feel very carefully. These, however, widen as the bird becomes adult, until they may be an inch or more apart—wide enough to allow the egg to pass through.

This, of course, is no new theory, though I do not know whether it has been tried on Parrots before. Many pigeon fanciers have sexed their birds by this method; but a well-known fancier who keeps nearly every variety of pigeon known, told me that in nine cases out of ten it might be correct, but in the tenth case you may get a male with the pelvic bones wide apart. But a bird in that condition was useless for breeding with, showing, I think, that this must be due to some congenital condition due probably to in-breeding, or breeding in semi-captivity, or some such cause.

But one has not to contend with this in Parrots. The Parrots that come to this country are all wild birds, which have bred in their own native land, and under their natural conditions.

In my live birds I have never made a mistake, but I was very anxious to prove this method by examining the pelvic bones

Text-figure 1.

BLUE FRONTED AMAZON

♂　　　　　　　　　♀

ROSE CRESTED COCKATOO

♂　　　　　　　　　♀
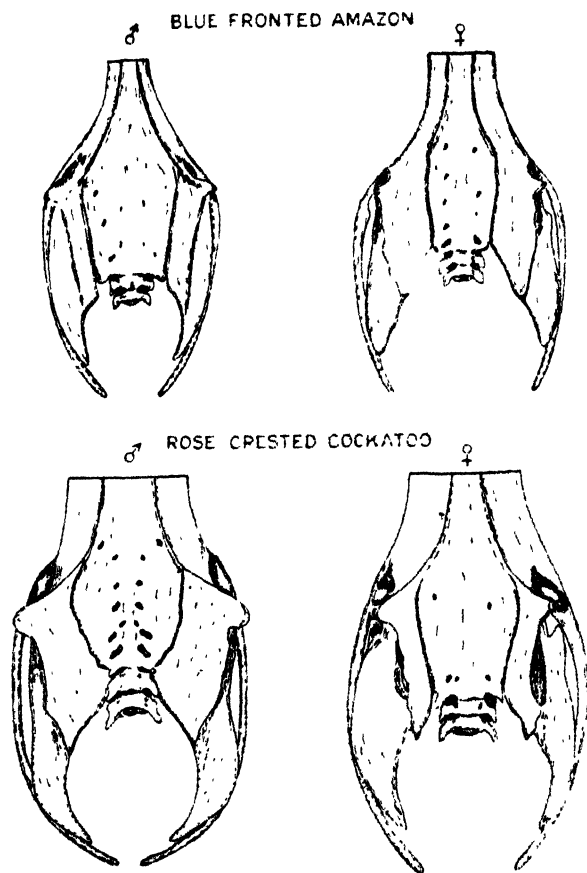
Pelvis of Male and Female Parrots.

of dead birds. I cannot thank the Zoological Society warmly enough for all the facilities granted, and for allowing me the privilege of working in their Prosectorium and examining the Parrots that have died in the Gardens: especially would I like to thank Mr. Hicks, who has helped me in every possible way

by preparing and keeping specimens he thought would be of use to me. I was anxious to wait until I could procure the pelvic bones of a true pair of Blue-fronted Amazon Parrots, and I have had a long wait. First of all, Parrots are fairly long-lived and do not die every day, and, secondly, those that did die proved to be all females.

Everyone who keeps a Parrot thinks they have a male bird, until one fine day it astonishes them by suddenly laying an egg. The fact is that male Parrots in this country are extremely rare, and the question is--*Why*? I think there are two reasons : first, they are more difficult to catch, and, secondly, when caught they are far more delicate. I believe if one could examine the crates of birds that come over, one would find that those which die on the voyage would prove to be mostly male birds.

Out of the twenty-five Amazon Parrots that I have kept, I have only had five males, and, for my own part, I have found them far more delicate, especially when first imported, than any female, and they need all one's care and resources to bring them round ; once acclimatised they seem all right. But this, I think, accounts for their extreme scarceness. Mr. Arthur, in his little book ' Parrots for Pleasure and Profit,' states that out of a number of Grey Parrots he had for post-mortem examination he never had a single male.

I have waited three years for the pelvic bones of a male Blue-fronted Amazon Parrot. They measure 9 mm. apart, while those of the female measure 25 mm. In the dead specimen the bones of the male are widened ; they do not meet as they feel to do in the live bird, and in a way one may say this is unsatisfactory : but I think there is much cartilage at the terminus of the bone which in the process of maceration comes away, and that this accounts for the widening.

The question may be asked, how one knows males from females in Parrots whose plumage is the same : but when one keeps several together, there are distinguishing features by which one may know.

The males, as a rule, are smaller, more compact birds, the females being a good deal larger, and the green of the feathers is generally a deeper, richer colour than in the females.

Also the males have a characteristic which I have never seen in a female. They become extremely restless towards roosting time, and often scream. Probably in their native state they are the first to leave the feeding grounds, and make for the trees where they mean to pass the night. The female may and can scream terribly, but she may do it at any time of the day, while the male waits until it is time to go home to bed and even then the noise does not last very long.

I have no experience whether this method of sexing applies to all birds—this has yet to be investigated ; but I have the

pelvic bones of a pair of the Common Pea-fowl, the measurements of which I have inserted at the bottom of the following table :—

Width of Pelvic Bones in Parrots.

	Male.	Female.
Blue-fronted Amazon	9 mm.	25 mm.
Rose-crested Cockatoo	3 ,,	10 ,,
Red and Blue Macaw ..	8 ,,	14 ,,
Roseate Cockatoo . ..	14 ,,	21 ,,
Mueller's Parrot	15 ,,	20 ,,
Alexandrine	5 ,,	22 ,,
Quaker Parrakeet . .	8 ,,	14 ,,
Rosy-faced Love-Bird . . .	7 ,,	14 ,,
Common Pea-fowl . . .	23 ,,	40 ,,

35. The Skull of the Dicynodont Reptile *Kannemeyeria*.
By HELGA S. PEARSON, M.Sc., F.Z.S.

(Text-figures 1–18.)

Kannemeyeria is the large Dicynodont reptile from the Upper Beaufort beds of the Karroo system of South Africa. All the Dicynodonts so far found in these beds can be placed in this genus, which is thus the very last of the family known to us in South Africa†. As Haughton tells us when describing a new species of *Kannemeyeria* in the ' Annals of the South African Museum,' 1915, the genus was founded by Seeley in 1908 on the skull of a large Anomodont found by Dr. Kannemeyer near Burghersdorp. This was a very imperfect and battered skull, with its nasals broken short, so that Seeley named it *Kannemeyeria proboscoides*, owing to a mistaken belief that it had had a proboscis. It is now No. R. 3593 in the British Museum, and has associated with it the greater part of the rest of the skeleton, all in an equally bad state of preservation. The skull Watson [1912] believed to correspond with that of *Dicynodon simocephalus*, a species founded by Weithofer in 1888 on an imperfect skull, of which he gave a figure and description.

The condition of Seeley's type *Kannemeyeria* skull is hardly such that its species can be satisfactorily determined, but it shows the general nature of the palate fairly clearly, and when measurements are taken of this, they are found to correspond almost exactly with the palatal measurements of the skull of a mounted skeleton of *Kannemeyeria* (R. 3739) in the galleries of the British

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† Professor Watson has pointed out to me that there are certain bones f om the Trias of the United States of America which bear a very strong resemblance to those of the large Dicynodonts such as *Kannemeyeria*, and suggest that this family had reached America before becoming extinct. These bones are *Placerias hesternus* Lucas (Proc. U.S. Nat. Mus. vol. xxvii. 1904, plate iv.), a humerus from the Trias of Tanner's Crossing on the Little Colorado River, Arizona, and *Eubrachiosaurus browni* Williston (Journ. of Geol. vol. xii. 1904, pp. 690–94), a humerus and a fragmentary pelvis and scapula from the upper part of the Triassic Red Beds, Popo Agie River, Wyoming. Lucas has compared the *Placerias* humerus with *Pariasaurus*, Williston the humerus of *Eubrachiosaurus* with the Deinocephalian *Tapinocephalus*. Von Huene, in his paper on *Erythrosuchus* [1911, pp. 48 & 49], reproduces their figures, discusses whether the bones may not have belonged to his new order of *Pelycosimia*, and confesses that the long, narrow scapula of *Eubrachiosaurus* reminds him of an Anomodont; his restored outline of the pelvis of *Eubrachiosaurus* seems entirely unwarranted, the existing dorsal border of the fragment being really the true edge of the pelvis, which is thus also exceedingly Anomodont. The humeri of both forms, with their expanded ends flattened in planes at an angle to one another, their antepicondylar foramina, and the shape of their condyles, are also essentially those of a large Dicynodont.

Museum ; the remaining bones of the two skeletons also corre-
spond very closely. This last skull (text-figs. 1, 2, & 7) is of
about the same size as Weithofer's *Dicynodon simocephalus*, but a
comparison with Weithofer's figures at once makes it clear that
they are very different, the most obvious difference lying in the
much steeper angle at which the parietal crest in No. R. 3739
rises from the parietal foramen, and in the whole shape of that
crest. It is true that the parietal crest in R. 3739 has been much
broken and crushed, but, even so, it was evidently not far from

Text-figure 1.

Partially reconstructed lateral view of the skull belonging to the mounted skeleton
    of *Kannemeyeria* in the British Museum, Nat. Hist. (No. 3739). One
    quarter actual size.

Bas.= Basisphenoid. Fr. = Frontal. Jug. = Jugal. Lach. = Lachrymal. Lach.
    For. = Lachrymal foramen. Max. = Maxilla. Nas. = Nasal. P.Max. = Pre-
    maxilla. P.Orb. = Postorbital. Par. = Parietal. Post.Temp.For. = Posterior
    temporal foramen. Pr.Fr. = Prefrontal. Pro. = Proötic. Pt. = Pterygoid.
    Qu. = Quadrate. Qu.J. = Quadrato-jugal. S.Max. = Septomaxilla. Squam. =
    Squamosal.

the shape it has been restored to with plaster, and of a peculiar
type, quite different from that in *Dicynodon simocephalus*. The
latter may well be placed in Seeley's genus, however, and indeed
has already been referred to as *Kannemeyeria simocephalus* by
Broom [1913, p. 452].
    In 1899 Broom created the species "*Dicynodon*" *latifrons* for
the fragment of a skull from the Upper Beaufort beds which he
said appeared to be very similar to that of *D. simocephalus*, but

narrower across the maxillary region (though I find that the width is very susceptible to alteration by crushing) and with orbits directed more laterally and less frontally.

Haughton's photographs of the skull for which in 1915 he created the species *Kannemeyeria erithrea* are very similar to Weithofer's drawings of *K. simocephalus*, though again not so broad across the maxillary region. He attempts no comparison.

Text-figure 2.
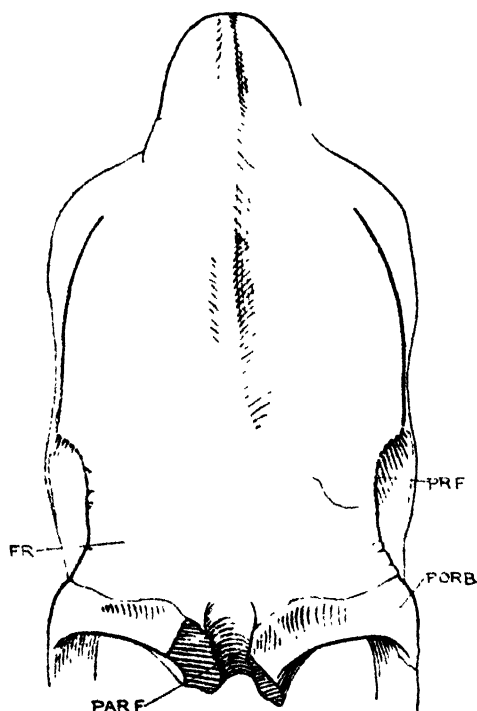
Dorsal view of anterior half of the same skull as in text-fig. 1.
One quarter actual size.

FR. = Frontal.   P.ORB. = Postorbital.   PAR.F. = Parietal foramen.
PR.F. = Prefrontal.

In 1917, in his ' Descriptive Catalogue of the Anomodontia,' he lists two species of *Kannemeyeria*—the *K. erithrea* which he had described two years earlier and Broom's *K.* (*Dicynodon*) *latifrons*. He does not refer to *K. simocephalus*, and again makes no comparisons.

In the British Museum, Natural History, there are several imperfect skulls from the Upper Beaufort beds which may all

be referred to the genus *Kannemeyeria*, but some of which
are clearly quite distinct from those just mentioned. The
one which I have drawn in text-figs. 10 and 11 belongs to Prof.
D. M. S. Watson; it has no palate, but, except for the quadrate
region, is almost complete on the left side. A distinctive feature
of the skull is the well-developed ridge running up the centre of
the nasal region and ending in a pronounced knob at or near
to the fronto-nasal suture. No. R. 4711, the fragmentary and
weathered anterior end of another skull in the British Museum,
has a similar ridge in the nasal region, and appears to correspond
very closely with Prof. Watson's skull. These two skulls are of

Text-figure 3
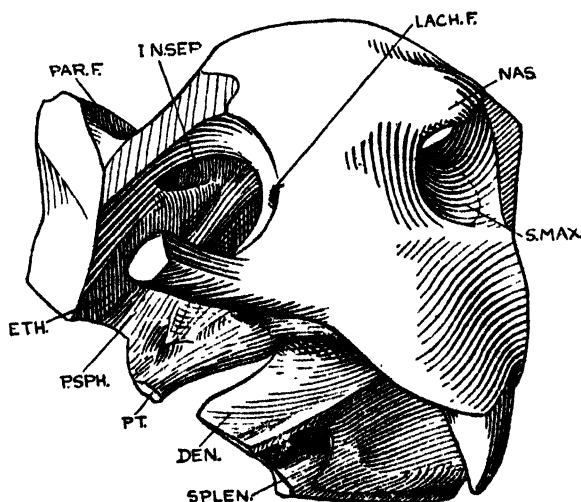
Lateral view of the fragment of a skull of another species of *Kannemeyeria* in the
　British Museum (No. 3742, "*Sagecephalus pachyrhynchus*" Jaeckel).
　One quarter actual size.

ETH.=Ethmoid. I.N.SEP.=Internasal septum. LACH F.=Lachrymal foramen.
　NAS.=Nasal. P.SPH.=Parasphenoid. PAR.F.=Parietal foramen. PT.=
　Pterygoid. S.MAX.=Septomaxilla. SPLEN.=Splenial.

approximately the same length as that of *K. simocephalus*, though,
judging from Weithofer's figures, not nearly so broad at any part
of their length. The angle which the parietal crest makes with
the frontal region is obtuse, as in *K. simocephalus*, *K. erithrea*, and
K. latifrons, and the whole build of the skull is very similar to
that of these three species. *K. simocephalus*, however, does not
appear to have the median ridge on the nasals which Prof.
Watson's skull has, while *K. latifrons*, which has it, though to a
less marked degree, is a very much smaller skull, not much more
than half the size of these two. *K. erithrea* is larger than any of

them; it has a median ridge on the snout, but this extends back only as far as the front of the orbit.

There is yet another type of *Kannemeyeria* represented in the Seeley collection in the British Museum. This is No. R. 3742, comprising a battered and somewhat contorted anterior end of a skull as far back as the region of the parietal foramen, and with the front end of the lower jaw attached.

It is the one which I have drawn in text-figs. 3 and 4, and is plainly very much broader and more massive than any of the others, while the frontal region arches up much more steeply in front of the parietal foramen. Jaeckel figured this skull in ' Die Wirbeltiere' (fig. 209, p. 191), making it the type of a new genus, " *Sagecephalus*," and a new species, " *pachyrhynchus*."

Text-figure 4.
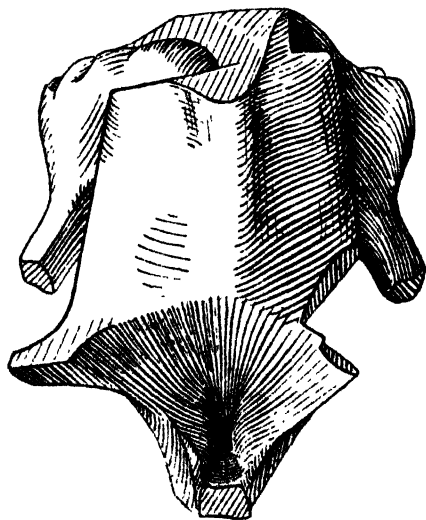
Dorsal view of the same skull fragment as in text-fig. 3.
One quarter actual size.

Considering how extremely fragmentary and ill-preserved are all these skulls in the British Museum, while Weithofer's and Broom's types are apparently not much better, it seems of little value to assign them to named species or to do more than point out the more obvious differences and resemblances as above. They are usually too distorted to admit of a wide range of even approximately accurate measurements, and without a wide range it would be impossible to compare so many fragments, which not only represent different parts of the skull, but are themselves imperfect and in different states of preservation.

The following descriptive account is based mainly on the two best skulls available to me: No. R. 3739, belonging to the

mounted skeleton in the British Museum, and Prof. Watson's skull. It is helped out by a study of the other British Museum fragments just mentioned. It is concerned not with the characters which differentiate species, such as differences in size and proportions, but with the more fundamental characters which all these skulls possess in common. Some of these will be characters found in all Dicynodont skulls, some, which I shall attempt to select and summarize at the end of the paper, will be those peculiarly characteristic of the Upper Beaufort Dicynodonts, and apparently representing the height of Dicynodont specialization.

The characteristics of a typical Dicynodont skull have become known to us through a whole series of writings, from the earliest description by Owen in 1845 of the first Dicynodonts sent over from S. Africa by A. G. Bain, to von Huene's recent paper in the ' Palæontologische Zeitschrift,' 1922. The Sollas' in 1913, in their paper entitled "A Study of the Skull of a *Dicynodon* by means of Serial Sections," gave a summary of the work up to that date on the structure of the skull of these animals. Owen, Huxley, Cope, Seeley, Lydekker, Newton, and Broom, each in turn had contributed something new. Then came the Sollas' themselves, with their new method of grinding the skull into serial sections; they finally settled several previously debated points and made further new contributions. In the same year [1913] v. Hoepen gave figures and a description (in Dutch) of the skull of "*Oudenoden*" *latirostris* Owen. Since then there have been various papers by Broom and Haughton, mainly concerned with the differentiation of species from the now enormous number of Dicynodont skulls in the collections. This work of theirs, especially Haughton's 'Catalogue of the Anomodontia' [1917], lays stress on the large and exceedingly interesting variety of types of Dicynodont reptile which existed in South Africa during uppermost Permian and lowest Triassic times. The only recent purely morphological work that I know of is the description which v. Huene gives in the paper just mentioned [1922] of an evidently unusually beautifully preserved little skull of *Dicynodon sollasi* Broom. He figures its dorsal, lateral, palatal, and occipital aspects, and is able to show nearly all the sutures and also (rather unusual) the slender epipterygoid bone in position.

To all these accounts my own description of *Kannemeyeria* can add little new, especially as the material is so much more fragmentary, weathered, and crushed than much of theirs. Fragmentary and broken material, however, often shows up from a new point of view parts not easily accessible in a complete skull, and from such I have taken text-figs. 5, 9, 13, 14, and 18; these aspects, I think, have not been figured before, although their component parts may have often been described. The many broken surfaces in my material has also, from the sections which they give, made it much easier to understand what I have had to describe.

The work was started and most of the figures drawn in pencil three years ago under the guidance of Prof. D. M. S. Watson. Since then it has been continued, with an interval of rather over a year, at the same time as work published in another paper on the description and restoration of the rest of the skeletal material associated with the *Kannemeyeria* skull No. 3793. Throughout this time I have made much use of Prof. Watson's experience. During the earlier part of the work I was assisting in the Department of Anatomy under Prof. J. P. Hill, and it was owing to his kindness that I was able to spend a part of my time at the British Museum.

I am further indebted to the late Dr. C. W. Andrews for the supply of my needs at the Museum, and also for some very useful criticisms of the drawings.

THE POSTERIOR REGION OF THE BRAIN CASE.

The details of this region are shown in one or other of several specimens; sutures are not traceable. Text-fig. 5 is drawn chiefly from Prof. Watson's skull, but gaps are filled in from two other fragmentary brain cases.

The dorsal surface of the occipital condyle is broadly grooved. At the level of the *foramen magnum* the walls of the brain case rise from the sides of this groove, inclining inwards a little towards one another, to a height which is about twice as great as the width of the groove itself; they then incline inwards more rapidly to meet above the foramen. The *foramen magnum* has accordingly the high and narrow shape characteristic of Dicynodont reptiles. This shape corresponds with that of the brain cavity, since the walls of the latter continue almost straight forwards from the *foramen magnum*, still slightly inclined towards one another above, so that they form an almost wedge-shaped arch.

The floor of the brain cavity is a strong ridge, continuous behind with the floor of the groove on the occipital condyle, and in front flattening out on the dorsal surface of the basisphenoid, where the latter bends upwards behind the pituitary fossa. Between the ridge and the base of the side wall of the brain case lies on either side a wide and irregular cleft, leading behind into the mouth of the wide vagal canal, further forwards into the cavity for the inner ear. The vagal canal leads backwards and outwards in front of the condyle, and is joined about midway in its course by a narrower canal for the twelfth cranial nerve, which pierces the exoccipital just at the mouth of the *foramen magnum*.

In the floor of the inner ear cavity lie two recesses, separated from the mouth of the vagal canal by ridge-like rims. The more mesial of these, a basin-shaped pit, presumably housed the cochlea; it has apparently no forward extension within the bone. The other recess, lying immediately external to the cochlea, is the

inner opening of the long tube which leads downwards from the vestibule to the *fenestra ovalis* at the extremity of the basisphenoidal tuber. In the side wall of the inner ear cavity are further recesses for the ampullæ of the semicircular canals and a groove for the *sinus communis*. Behind and in front, these are overhung by bony ledges which cut them off from the vagal canal and the

Text-figure 5.
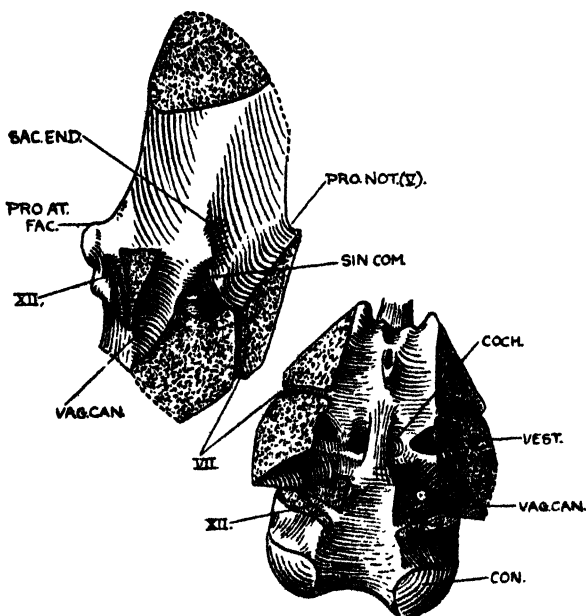
The floor and left side wall of the posterior end of the brain case of *Kannemeyeria*, taken chiefly from Prof. Watson's skull, which is broken much as in the figure. The plane of the lower half of the brain case side wall is really bent outwards at an angle of about 30° from the plane of the upper half; they are drawn as though in the same plane to avoid foreshortening. One half actual size.

COCH.=Pit for cochlea. CON.=Condyle. PRO.AT.FAC.=Articular facet for pro-atlas. PRO.NOT.(V.)=Proötic notch for passage of trigeminal nerve. SAC.END. = Depression marking position of saccus endolymphaticus. SIN.COM.=Groove for sinus communis. VAG.CAN.=Vagal canal. VEST.= Vestibule. VII.=Canal for facial nerve. XII.=Canal for hypoglossal nerve.

groove for the trigeminal nerve. A short distance in front of the vestibular canal the small canal for the facial nerve runs downwards and outwards through the proötic.

These conditions of the inner ear and posterior cranial nerves in *Kannemeyeria*, as Haughton also found in *K. erithrea*, correspond in general with those which Broom found in his cast of the

brain cavity of *Dicynodon* [1912]. There is the same long canal leading from the vestibular cavity to the *fenestra ovalis*, and there is a single canal for the twelfth cranial nerve uniting with the vagal canal before the latter leaves the skull. Broom, however, found "no trace of a cochlea," whereas in *Kannemeyeria* its position is marked by a well-defined pit.

In front of the inner ear region the floor of the brain case begins to slope upwards, the median ridge flattening out on the surface of the slope, though a little further forwards a new and narrower ridge arises in the mid-line. On either side of the mid-line in this region, and continuous behind with the inner ear cavity, is the wide groove for the trigeminal nerve leading up to the usual notch in the anterior edge of the proötic.

On the inner surface of the side wall of the brain case, where this wall overhangs the inner ear cavity, and in the same transverse plane as the ampullæ for the anterior and external semicircular canals, is a shallow depression bounded behind by a ridge. From the ventral corner of the depression, which has the shape of an acute-angled triangle with its base upwards, a small groove appears to run round into the dorsal end of the *sinus communis*. The depression very possibly marks the position of a large endolymphatic sac, the groove that of its duct. Except for this depression the sides of the brain cavity are smooth and flat.

At the level of the proötic notch the upwardly sloping dorsal surface of the basisphenoid terminates abruptly, and the bone presents an almost vertical anterior face, in front of which the infundibulum must have projected down in life. At the base of this vertical face lies the pituitary fossa, a depression in the dorsal surface of the parasphenoid. The latter is here indistinguishably fused with the basisphenoid and closely embraced by the pterygoids, which meet each other below it, but further forwards, where these separate, rises above them as a slender girder supporting the ethmoid on its dorsal edge.

The internal carotid arteries open into the pituitary fossa from below, sometimes separately, sometimes by a single canal.

THE ETHMOID REGION OF THE BRAIN CASE.

The structure of the inner wall of the orbit is not shown well in any of the *Kannemeyeria* material that I have seen. In both R. 3739 and in Prof. Watson's skull it is almost entirely broken away and in Seeley's type-skull (R. 3593) it cannot be seen. In the massive R. 3742 the greater part of it is still left, but in a very bad state of preservation.

Although the general structure of this region is well enough known, it has never, I believe, been adequately figured. Therefore I am including in this paper a drawing of it taken from a free-hand sketch of a skull of *Dicynodon moschops*, No. 5325, in the American Museum of Natural History. The sketch was made two years ago without the intention of publishing, so no

accurate measurements were taken. Broom [1913] has already
figured the pineal region and the lateral view of the skull, but
he did not show or refer to the intra-orbital structure. To show
this latter I have in my sketch omitted the zygomatic and post-
orbital arches (text-fig. 6).

The antero-ventral part of the ethmoid, a median bony inter-
orbital septum, is seen resting on the dorsal edge of the para-
sphenoid, while dorsally the bone is cleft to make a channel for
the fore-brain ; this channel is completed by the frontal bones,
which roof it in above and send down vertical flanges to meet
the ethmoid and complete the lateral walls. Behind the frontal

Text-figure 6.
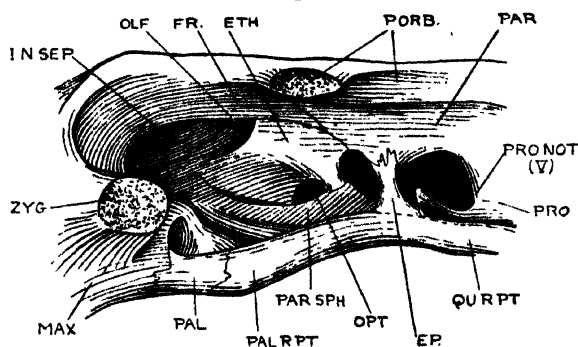
Dicynodon moschops (American Museum of Natural History, No. 5325). Free-
hand sketch of anterior part of the brain case as seen from without with the
zygomatic and postorbital bars removed. About one half actual size.

Ep. = Epipterygoid. Eth. = Ethmoid. Fr. = Frontal. I.N.Sep. = Internasal
septum. Max.=Maxilla. Olf.=Position of olfactory lobe of brain.
Opt.=Optic foramen. P.Orb.=Postorbital. Pal.=Palatine. Pal.R.Pt.
=Palatine ramus of pterygoid. Par.=Parietal. Par.Sph.=Parasphenoid.
Pro.=Proötic. Pro.Not. (V.)=Proötic notch for trigeminal nerve.
Qu.R.Pt.=Quadrate ramus of pterygoid. Zyg.=Anterior end of zygomatic
arch.

the ethmoid meets the descending flange of the parietal, the outer
surface of which is partly overlapped by the postorbital. The
hinder edge of the ethmoid lies in a transverse plane anterior to
the pineal foramen and just posterior to the postorbital arch. It
is a free edge extending from the descending flange of the
parietal above to the parasphenoidal bar below. The parasphe-
noidal bar is here elevated into a high median projection, just
posterior to the interpterygoid vacuity, but far above the level of
the pterygoids. A little way in front of the projection the
foramen for the optic nerve makes a small gap between parasphe-
noid and ethmoid ; in front of this the two bones are again in

contact, the median septum of the ethmoid resting in a groove on the dorsal edge of the parasphenoidal bar.

Behind the ethmoid, which in life must have housed the cerebral hemispheres, there is a great gap in the lateral wall of the brain case, extending from the posterior edge of that bone to the anterior edge of the proötic behind the proötic notch for the trigeminal nerve. In this part of the brain case there must in life have lain the thalamencephalon and most of the mid-brain. Viewed from the side it is partly covered by the narrow epipterygoid; this rests on the pterygoid below, just lateral to the pituitary fossa, and has a suture above with the descending flange of the parietal. The floor of this part of the brain case is the parasphenoid, hollowed out behind by the pituitary fossa, where it meets the basisphenoid; the infundibulum must have rested on this floor.

This brings us back to the posterior part of the brain case described in the last section.

In the roof of the median, unwalled part of the brain case a very wide duct leads upwards to the pineal foramen. This lies immediately posterior to the ethmoid bone between the descending parietal flanges of either side and just in front of where these meet the epipterygoid. Behind this these two flanges no longer enclose a median channel as do the descending flanges of the frontals in the orbital region, but are pressed together in the middle line, their ventral edges forming the roof of the brain case.

At the anterior end of the brain case the median ethmoidal septum joins the bony internasal septum. Dorsal to this, where the ethmoid is cleft, each side of the cleft has a free anterior edge, showing the internasal septum standing up as a vertical wall in the middle line; on this in life must have rested the olfactory lobes of the brain, the olfactory nerves passing downwards and forwards on either side of it into the nasal cavities.

With this description of the ethmoidal region of the brain case in *Dicynodon moschops* the massive and contorted *Kannemeyeria* skull No. 3742, as far as it can be made out, agrees (text-fig. 3).

THE PALATE.

Text-fig. 7 of the palate of *Kannemeyeria* is based on the skull of the mounted skeleton, No. 3739. Since in that skull the palatines in the region of the posterior nares are broken, and the prevomers lost, I have reconstructed these from Seeley's type-specimen, which, however, does not show the sutures. The British Museum specimens agree essentially with Haughton's description of *K. erithrea* [1915].

In the primitive *Endothiodon* palate, as figured by Watson in P. Z. S. 1921, the anterior ends of the pterygoids meet the posterior ends of the palatines in a straight suture well behind the anterior border of the temporal fossa, and there

Text-figure 7.
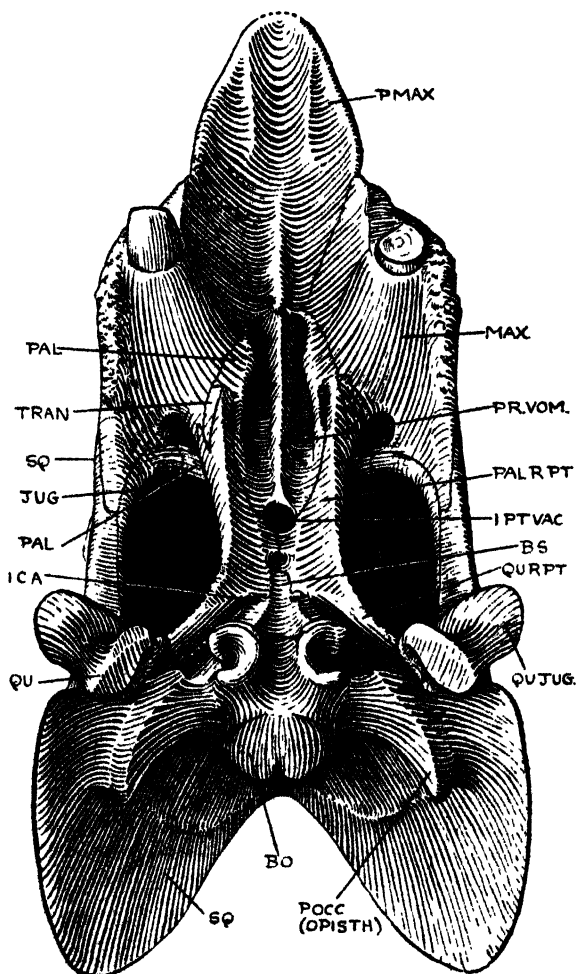
Reconstructed palatal view of the skull of the British Museum *Kannemeyeria*
No. 3739. One quarter actual size.

B.O. = Basioccipital.   B.S. = Basisphenoid.   I.C.A. = Internal carotid artery.
I.Pt.Vac. = Interpterygoid vacuity. Jug. = Jugal. Max. = Maxilla. P.Max.
= Premaxilla. P.Occ. (Opisth.) = Paroccipital process of opisthotic. Pal. =
Palatine. Pal.R.Pt. = Palatine ramus of pterygoid. Pr.Vom. = Prevomer.
Qu. = Quadrate. Qu.J. = Quadrato-jugal. Qu.R.Pt. = Quadrate ramus of
pterygoid. Sq. = Squamosal. Tran. = Transpalatine (ectopterygoid).

is apparently no overlapping. In the various types of *Dicynodon* the pterygoids overlap the palatines to a greater or lesser extent. In *Kannemeyeria* there appears to be an extreme of overlapping, for the pterygoids reach forwards far in front of the temporal fossa to the region where the maxillæ curve downwards round the root of the tusk : they carry forwards with them, wedged into their forked anterior ends, the now very much reduced transpalatines, which thus lose all connection with the elements of the zygomatic arch, the jugal being met by the palatine and by the maxilla directly.

Posteriorly the pterygoids reach back to the quadrates by their quadrate rami, the tips of these being wedged in between the quadrates and the ends of the paroccipital processes which abut on them.

In their middle region the pterygoids meet in the mid-line beneath the posterior end of the parasphenoid, having a suture with the basisphenoid as it rises up to become continuous with the latter just in front of the internal carotid foramina. They touch for a short distance only, and in the suture between them is a foramen, presumably for a nutritive blood-vessel. Along this region there is in some, at any rate, of the more primitive Dicynodonts a median ridge (see, for instance, v. Huene's fig. 3 of *Dicynodon sollasi*) ; *Kannemeyeria*, on the contrary, has a shallow groove along this line.

In front of this the pterygoids diverge once more as the two palatal rami, and leave between themselves and the posterior end of the prevomers a small round interpterygoid vacuity. Whether the prevomers separate from one another posteriorly round the anterior edge of this vacuity, each touching the pterygoid of its own side, as happens in more primitive skulls (see, again, v. Huene's fig. 3), cannot be certainly determined from the present material ; but well-marked sutures in R. 3739 seem to show that the palatines extend back along the dorso-medial surfaces of the pterygoids to the interpterygoid vacuity, touch the parasphenoid, and bend inwards towards each other to form at least a part of the anterior wall of the vacuity. Thus it would seem that in *Kannemeyeria*, not only have the pterygoids grown forwards, but the palatines also have had an active share in the process of overlapping by themselves growing backwards. The fusion of the prevomers to form a median ridge in the naso-pharyngeal passage has also continued backwards at the expense of the interpterygoid vacuity.

All these changes must add very greatly to the strength of the central part of the skull, a strength no doubt very desirable in view of the massive anterior end supporting the large tusks and the great pull which the pterygoid muscles must have exerted in manipulating the equally massive mandible. A dorsal view of the more primitive type of palate may be seen in text-fig. 8 of a young Dicynodont skull from the top of the Nieuveldt's escarpment, Hottentot River, Beaufort West, belonging to

Prof. Watson. In this the interpterygoid vacuity is much longer, the prevomers being separated from each other posteriorly for a much greater distance, while the pterygoids and palatines overlap each other but little; the ventral view of this palate is essentially similar to v. Huene's figure of *Dicynodon sollasi.*

Text-figure 8.
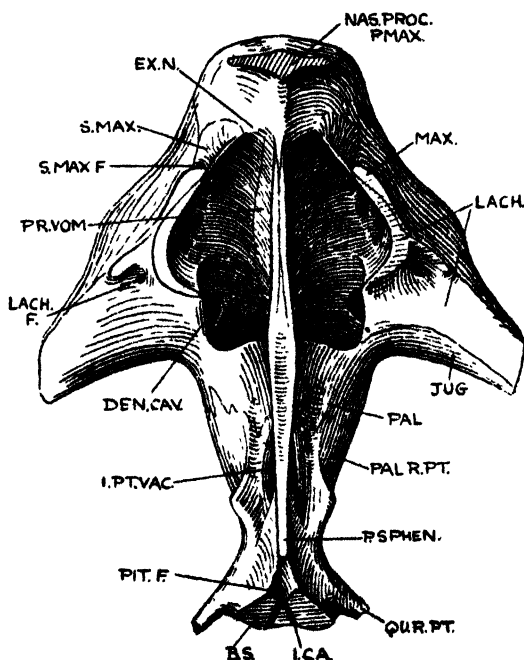
A young Dicynodont skull from the top of the Nieuveldt's escarpment, Hottentot River, Beaufort West. Palate and interior of nasal cavity viewed from above, with brain case and roofing bones removed. One half actual size.

B.S. = Basisphenoid.   Den.Cav. = Cavity for root of tusk.   Ex.N. = External naris. I.C.A. = Foramen for internal carotid artery.   I.Pt.Vac. = Interpterygoid vacuity.   Jug. = Jugal.   Lach. = Lachrymal foramen.   Max. = Maxilla. Nas.Proc.P.Max. = Nasal process of premaxilla.   P.Sphen. = Parasphenoid. Pal. = Palatine.   Pal.R.Pt. = Palatine ramus of pterygoid.   Pit.F. = Pitutiary fossa.   Pr.Vom. = Prevomer.   Qu.R.Pt. = Quadrate ramus of pterygoid. S.Max.F. = Septomaxillary foramen.

The palatal rami of the pterygoids in *Kannemeyeria* are two stout bars with ridge-like ventral edges. They form with the vertical plates of the palatines, which overlap their dorsal edges on the medial surface, the side walls of the deep, wide naso-pharyngeal passage. This passage is roofed partly by the palatines arching over above it and partly by the prevomers, but sutures are indeterminable. The passage is divided longitudinally by

the high but slender prevomerine ridge, which meets the hard secondary palate in front.

In front of the temporal fossa the palatine sends out a lateral process to meet the jugal. This process passes dorsal to the anterior end of the pterygoid and to the transpalatine which are carried unusually far forwards, as stated above.

On the palate, mesially to the pterygoids, the palatines extend forward in front of these to the anterior end of the naso-palatine groove and in this region form not only roof and side wall to the latter, but also send inwards from the ventral edge of that side wall a horizontal shelf. This shelf extends about half-way across the groove, its free inner edge curving inwards towards the prevomerine ridge, together with which it may in life have supported a soft secondary palate. At the place where the posterior end of this shelf arises from the vertical plate of the palatine there is a depression in the sharp angle between the ventral surface of the shelf and the vertical median surface of the anterior extremity of the pterygoid ridge.

It has been pointed out by Watson [1921] that the hard secondary palate in Dicynodonts is formed not in the mammalian manner, of which he has traced the evolution, but by a method identical with that in the Chelonia. The roof of the naso-pharyngeal duct of mammals represents the original surface of the palate. In Dicynodonts the deep groove into which the posterior nares open has been excavated in the original palate, "which is roofed by a great forward growth of the prevomers over the region formerly occupied by the large posterior nares."

In *Dicynodon* and in *Kannemeyeria*, as in *Endothiodon*, the palatal plate of the premaxillæ forms a broad, hollowed surface at the anterior end of the palate in front of the maxillæ. It extends forwards some way in front of the maxillæ, and it extends backwards between them to the anterior end of the naso-palatine groove, thus separating their palatal portions from each other. Anteriorly, in front of the maxillæ, there are two broad, longitudinal ridges dividing its hollowed surface into three parallel grooves, of which the central one is deeper and wider than the two on either side. These ridges apparently rubbed against the inner surfaces of those bounding the median groove which is present on the dorsal surface of the massive symphysis of the lower jaw. This groove and the median groove on the premaxillæ thus form together a narrow channel, in which perhaps lay the anterior end of the tongue. The two lateral grooves on the premaxillæ received the ridged edges of the lower jaw which, in a side view with the jaws closed, are always seen to be overhung by the premaxillæ. The whole is usually supposed to have been covered by a horny beak.

Posteriorly the palatal plate of the premaxillæ bears the usual pronounced ridge ending behind in an elevated knob, with which is continuous the sharp and narrow ridge of the fused prevomers.

The palatal portions of the maxillæ are utilized almost entirely in supporting the great tusks. They project down round the roots of the latter far below the general surface of the palate, in which they play very little part, being excluded anteriorly by the premaxillæ, posteriorly by the anterior ends of the palatines. On the palate each meets the premaxilla, the palatine, the trans-palatine, and, for a very short distance only, the outer branch of the forked anterior end of the pterygoid, into which the trans-palatine is wedged. In the zygoma each maxilla sends back a process which reaches nearly to the postorbital bar, overlaps the jugal, and is overlapped by the squamosal which extends for-wards almost to the front of the orbit. There is the usual large foramen, bounded behind by the jugal and transverse process of the palatine, and separating the zygomatic part of the maxilla from the more strictly palatal part. It passes into the chamber surrounding the roof of the tusk, and is usually presumed to be for the transmission of a branch of the fifth nerve and accom-panying blood-vessels.

The alveolar border of the maxilla behind the tusk has a swollen and roughened edge.

The Nasal Cavity.

The shape of the nasal cavity is best seen in the skull fragment R. 4711, which appears to agree very closely with Prof. Watson's skull. This fragment is broken into several pieces, one of which is represented in text-fig. 9; it is of the front end of the snout as seen from above, with the roof of the nasal cavity and its right wall broken away. The break on the left side crosses the external naris at about half its height, so that in front the nasal process of the premaxilla is seen in section, behind the septo-maxilla and lachrymal. The lachrymal is sectioned almost along the line where the nasal and maxilla touch each other, these bones overlapping it on its outer surface and completely hiding it anteriorly in the external view of the skull: further back, where the lachrymal is exposed in front of the orbit, the break passes just above the lachrymal foramen.

Text-fig. 8, already referred to as giving a dorsal view of the palate of a young Dicynodont more primitive than *Kannemeyeria*, also shows the nasal cavity with its roof broken away at much the same level as in text-fig. 9; except in proportions and in one or two details it agrees very well with conditions in *Kannemeyeria*, and being in a much better state of preservation than R. 4711, helps to confirm the apparent structure of the latter.

The back of the nasal cavity has two openings to the exterior on each side. The more ventral of these is the posterior naris; it leads into the naso-palatine groove on the palate and is separated from the more dorsal opening, which leads into the orbit, by those parts of the palatine and prevomer which arch over towards each other, meeting and overlapping, to form the roof of this

groove. The opening from the nasal cavity into the orbit is thus bounded ventrally by this roof, which ends freely at the front of the orbit; laterally it is bounded by a free edge of lachrymal, dorsally by the small prefrontal, and mesially by the internasal septum. In other words, the anterior wall of the orbit is incomplete owing to the lachrymal, prefrontal, palatine, and ethmoid failing to meet each other.

Text-figure 9.
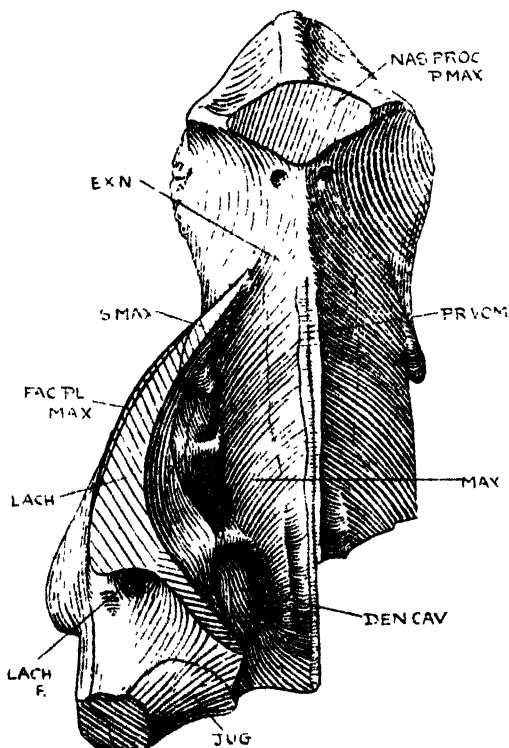
The nasal cavity of *Kannemeyeria* as seen from above in a fragment of the British Museum skull, No. 4711. One half actual size.

Fac.Pl.Max.=Facial plate of maxilla. Other lettering as in text-fig. 8. The dental cavity is here filled by the root of the tusk.

In the young *Dicynodon* skull (text-fig. 8) the bony internasal septum is high and slender. In it the paired prevomers embrace anteriorly a yet slenderer median septum arising from the palatal part of the premaxillæ. Behind this they come together for a short distance and then separate again to receive the anterior end

of the ethmoid, whose ventral edge is wedged between them, as is also the anterior end of the parasphenoid beneath the ethmoid.

In all the *Kannemeyeria* skulls where the nasal region is shown at all, the bony internasal septum has been broken off close against the floor of the nasal cavity, and the bones it is composed of are not distinguishable. The suture lines which mark the ventral edges of the prevomers within the nasal cavity in the young *Dicynodon* appear to be represented in R. 4711 by an irregularity on either side of the somewhat crushed nasal floor. The prevomer is here meeting the maxilla, which forms the rest of the floor of the cavity, but appears for only a short distance up its side wall, the rest of this being formed by the overlapping lachrymal. The latter extends forwards from the orbit to the hinder edge of the septomaxilla, lying within the facial plate of the maxilla.

In *Kannemeyeria*, as in the Dicynodonts described by the Sollas', the root of the great tusk is freely exposed in the nasal cavity; it forms the greater part of the posterior half of the lateral wall. In the young *Dicynodon* the tusks are as yet small in proportion to the size of the skull, and posterior to each there are two very small teeth close together on the alveolar border of the maxilla. Here the root of the tusk does not appear in the side wall of the nasal cavity, but there is the usual large gap between the lachrymal, maxilla, and palatine, where it would appear in older skulls.

The anterior half of the nasal cavity is of interest because it indicates the presence and position of an Organ of Jacobson. In front of the root of the tusk the cavity expands out to the side, its floor still arching up to the median septum, its side wall forming a steeper arch above it. In the lateral part of this wide anterior portion two hollows, separated from each other by a low ridge, lie in the angle between the side wall and the upwardly-arching floor. Screening the more posterior of these hollows from the root of the tusk is a bony wall, formed above by an inward projection from the lachrymal, below by a similar projection from the maxilla; this wall is the anterior wall of the cavity, called by the Sollas' "the dental chamber," in which the root of the tusk lies. The lachrymal bone external to the root of the tusk is perforated by the lachrymal duct; the nasal opening of this duct lies in the side wall of the nasal cavity, in front of the inwardly-projecting part of the lachrymal and above the posterior hollow. Just dorsal to the nasal opening of the lachrymal duct in front and to the root of the tusk behind is a well-marked ridge on the lachrymal bone, formed by the inner surface of that bone shelving abruptly outwards before curving up to meet the inner surface of the nasal.

The more anterior of the two hollows in the anterior part of the nasal cavity is immediately below and behind the external naris, from which it is separated by the inwardly-slanting septo-

maxilla. The septomaxilla slants inwards over this hollow in a plane that lies at an angle of about forty-five degrees to those of both the internasal septum and the floor of the nasal cavity: it thus ends anteriorly in contact with the latter, here formed by the premaxilla. It is a thin plate of bone, forming a floor to the nostril and bordered behind by the facial plate of the maxilla; at its postero-dorsal corner it rises up to form the hinder border of the nostril and touches the nasal, which overhangs the nostril, somewhat within the projecting lateral edge of that bone (text-figs. 1 & 10). Between this more upright postero-dorsal part of the septomaxilla and the facial plate of the maxilla behind it, there is in the young *Dicynodon* skull a very well-marked foramen leading from the exterior into the hollow just described. In *Kannemeyeria* there is a small pit externally in the same position, but I have not been able to prove satisfactorily that it is a foramen. It presumably corresponds with what Watson [1921, p. 75] has termed the " septomaxillary foramen" in other Theriodonts, suggesting that it might be of the nature of a second nostril associated with the Organ of Jacobson. The hollow into which it leads in *Dicynodon* and the similarly situated hollow in *Kannemeyeria*, separated as they are from the true nostril by the inwardly slanting antero-ventral part of the septomaxilla and marked off from the nasal cavity behind by a low ridge, certainly suggest the housing-place of an Organ of Jacobson. In *Kannemeyeria* there is, further, a small, conical, bony process projecting backwards into this hollow from its anterior wall and suggesting a support to such an organ, though this support in recent forms is usually given by a cartilaginous process from the nasal capsule. I have been unable to find any trace of a duct leading downwards from the hollow onto the palate, but the corner is not very accessible to exploration.

This interpretation of the position of the Organ of Jacobson is partly based on a comparison with the condition in a late embryo of the lizard *Lygosoma*, of whose skull I recently made a model [1921]. Here, again, Jacobson's Organ lies in the antero-ventral corner of the nasal cavity, and is roofed over by a slanting plate of septomaxilla, while from the latter bone again arises a small upright portion which reaches up to the roof of the skull. The main difference seems to be that in the young lizard the roofing-plate is hidden from without by the anterior wall of the cartilaginous nasal capsule, which covers in most of the gap between the facial plate of the maxilla behind and the nasal process of the premaxilla in front. This causes the inclusion within the lizard's nasal cavity of a space, floored in by the septomaxilla, which, even in Dicynodonts, is roofed by the overhanging nasal, but in them is without a lateral wall and widely open to the exterior. In the lizard there is nothing which really corresponds to a septomaxillary foramen, and a closer comparison between such distantly-related types is likely to be of little value.

TEMPORAL AND CIRCUM-ORBITAL BONES.

The sutures between these bones, as far as they can be determined, have been shown in text-figs. 1 and 10, the lateral views of R. 3739 and Prof. Watson's skull.

The zygomatic bar, which is long and narrow, is formed along its whole length by two closely-opposed strips of bone, the inner of which is the jugal, the outer the zygomatic process of the squamosal. The posterior end of the jugal is a splint of bone tapering to a point just anterior to the root of the zygomatic bar and on its inner surface; the main mass of the bar is here formed by the squamosal. About half-way along the zygoma is the base of

Text-figure 10.
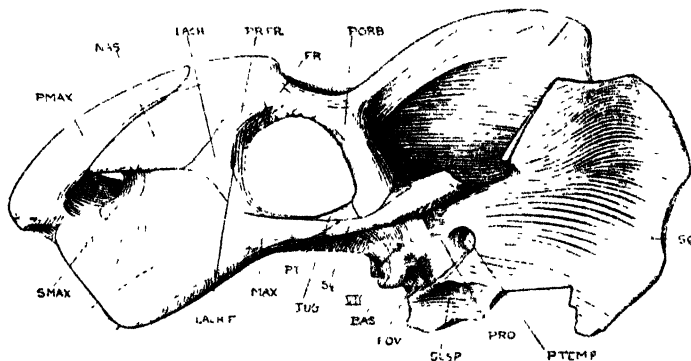
Lateral view of Prof. Watson's *Kannemeyeria* skull, with the sutures partly filled in from the British Museum skull, No. 4711. One quarter actual size.

Bas. = Basisphenoid.   F.Ov. = Fenestra ovalis.   Fr. = Frontal.   Jug. = Jugal. Lach. = Lachrymal.   Lach.F. = Lachrymal foramen.   Max. = Maxilla. Nas. = Nasal.   P.Max. = Premaxilla.   P.Orb. = Postorbital.   P.Tem.F. = Posterior temporal fenestra.   Pr.Fr. = Prefrontal.   Pro. = Prootic.   Pt. = Pterygoid.   S.Max. = Septomaxilla.   Sq. = Squamosal.   Susp. = Anterior surface of suspensorial plate of squamosal, hollowed out to receive wing-like portion of quadrato-jugal.   VII. = Foramen for facial nerve.

the postorbital bar, and against the inner surface of this the jugal is drawn up into a short, wide, supporting process. The jugal thickens in this region, and further forwards, beneath the orbit, it forms the main mass of the zygoma, the squamosal in turn being reduced to a thin, tapering splint, which, however, is remarkable in nearly reaching the anterior border of the orbit. A narrow process of the maxilla also takes part in the suborbital portion of the zygoma ; it is wedged in between the jugal on the inside and the anterior splint of squamosal on the outside, and appears between them on the ventro-lateral surface of the bar, extending posteriorly almost as far as the postorbital. Broom

[1914, p. 442] found a similar overlapping of squamosal and maxilla beneath the orbit in the big Lower Beaufort Dicynodont which he called *Eocyclops longus*.

At its anterior end the jugal meets the lachrymal, which rises up from it to form the anterior border of the orbit. The dorsal surface of the jugal is here somewhat expanded, its mesial border curving inwards to meet the palatine, there being, as pointed out in the description of the palate, no intervening transverse bone in these advanced Dicynodonts.

The postorbital bone forms the greater part of the postorbital bar. Its lower end meets the squamosal, and is flattened against the outer surface of the jugal, where that bone is produced upwards for a short way behind it. Above the jugal the postorbital is roughly triangular in section, with all the angles rounded and with the anterior angle bulging and roughened and transversely grooved, as is also the supraorbital ridge continuous with it. Dorsally, the postorbital meets the short postorbital process of the frontal, and itself sends backwards a long temporal process along the outer surface of the parietal crest, reaching and overlapping the squamosal posteriorly. There is no postfrontal.

The frontal bone forms only a small part of the roughened supraorbital margin. The anterior part of the latter is formed by the prefrontal, a small bone whose suture with the lachrymal is not very clear, but appears to be just at the antero-dorsal corner of the orbit. From the ventral surface of both frontal and prefrontal a plate of bone projects down to contribute to the inner wall of the orbit dorsally. As described in the section on the ethmoidal region of the brain case, the orbital plate of the frontal meets the dorsal edge of the ethmoid, while that of the prefrontal is continuous with the lachrymal in the anterior wall of the orbit; lachrymal, prefrontal, ethmoid, and palatine fail to meet, however, in the antero-mesial corner of the orbit, so that a gap is left through which the latter communicates with the nasal cavity, exposing to view the internasal septum.

The nasals are excluded from the border of the orbit by the prefrontals and lachrymals. They meet the frontals behind by a suture which lies at about the level of the middle of the orbit, being continuous with that between frontal and prefrontal, but which is usually hard to trace owing to the rough and pitted surface of the skull in this region.

The parietal crest reaches an extreme of height and compression in *Kannemeyeria*, and rises behind the parietal foramen at an angle of varying steepness. It arises from the frontal surface as two ridges enclosing a depression at the back of which lies the parietal foramen. The structure of this region is hard to determine. A small, median parietal bone is doubtfully situated at the bottom of the depression. On either side of the depression the posterior ends of the frontals appear to be drawn up onto the inner surfaces of the ridges as thin vertical sheets of bone ; they pass back on either side of the parietal foramen into the

parietal crest, apparently separating the anterior ends of the parietal bones from each other. I can find no evidence in the material available that they are received into clefts in the parietals as is usual in skulls of the less compressed type, but I cannot be quite certain that the thin vertical sheets of bone

Text-figure 11.
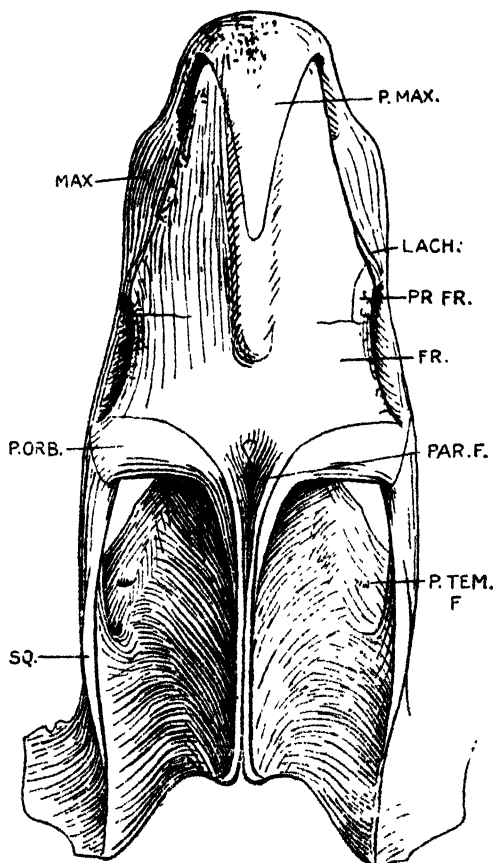
Reconstructed dorsal view of Prof. Watson's *Kannemeyeria* skull and of B.M. No. 4711. One quarter actual size.

PAR.F. = Parietal foramen. Other lettering as in text-fig. 10.

bounding the parietal foramen are not really the parietals, while the frontals are the bones passing laterally between these and the postorbitals, as Haughton finds in *Kannemeyeria erithrea*.

In the crest itself the parietals are represented by their narrow upturned edges only. They are tightly pressed against the thin

temporal flange of the postorbitals on their outer surfaces, but their dorsal edges are separated from each other by a cleft. Posteriorly, where they overhang the occiput, they separate from one another, following the outward curve of the squamosal, and the cleft between them widens out onto the deeply sunken occipital surface.

OCCIPUT.

Few of the occipital sutures are determinable in either R. 3739 or Prof. Watson's skull. In both of these skulls it is only the left-hand side of the occiput that is at all complete.

Text-figure 12.
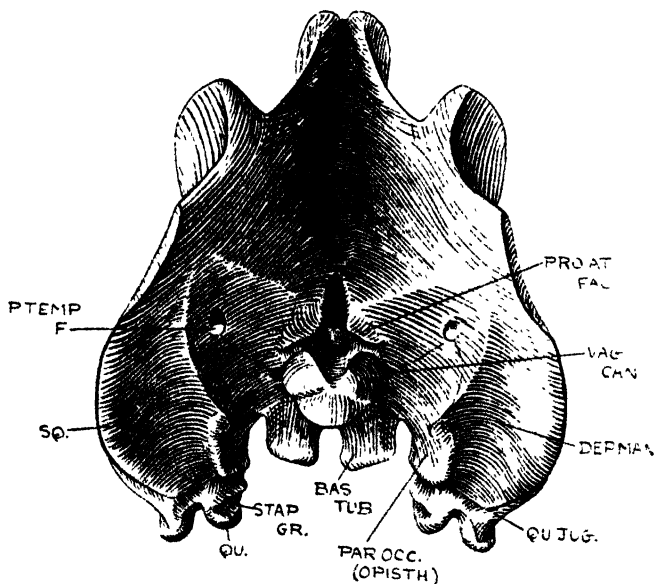
Reconstruction of the occiput of *Kannemeyeria*, taken chiefly from Prof. Watson's skull. Quadrates and quadrato-jugals added from the British Museum fragment, No. 3751. One third actual size.

Bas.Tub.=Basisphenoidal tubes. Dep.Man.=Groove for *depressor mandibuli* muscle. P.Tem.F.=Posterior temporal fenestra. Par.Occ.(Opisth.)=Paroccipital process of opisthotic. Pro.At.Fac.=Articular facet for pro-atlas. Qu.=Quadrate. Qu.Jug.=Quadrato-jugal. Sq.=Squamosal. Stap.Gr.=Groove on quadrate for outer end of stapes. Vag.Can.=Vagal canal.

Text-fig. 12 is a reconstruction taken chiefly from Prof. Watson's skull, which is much less crushed than the other, and, apart from the sutures, shows the general structure well. A curious feature of this skull is the shallow bay about half-way up

the usually smooth convex outer edge of the squamosal. This bay, seen in side view in text-fig. 10, has the appearance of a clean bite, but is evidently the genuine edge of the bone.

The high parietal crest of *Kannemeyeria* raises the occiput to a high, sharp angle dorsally. The great lateral wings of the squamosal are directed backwards at an angle of about forty-five degrees to the sagittal plane; the median line of the occiput, which dorsal to the *foramen magnum* is a shallow groove, is deeply sunken between them.

Break sections show that tabulars are present on the posterior surfaces of the squamosals and probably also an interparietal (dermal supraoccipital) in the middle line between them, but their outlines are not visible.

The paroccipital processes of the opisthotics, acting as struts to the suspensorium, are directed not only more backwards, but more downwards than in earlier Dicynodonts, leaving only a narrow cleft between their lower edges and the basisphenoidal tubera; this brings the quadrates nearer to one another than in the more primitive forms and further below the base of the cranium.

The posterior temporal fenestræ are very small. Each marks the dorsal boundary of the opisthotic and the lateral boundary of the exoccipital, the vagal canal probably also passing out between these two bones more mesially.

Just lateral to the *foramen magnum*, at rather less than half its height above the brain case floor, there are two little projecting shelves of exoccipitals on which the pro-atlas must have rested anteriorly.

The *foramen magnum* has already been described in connection with the brain case. The condyle is divided by two grooves into the usual three parts.

JAW ARTICULATION.

The relations in Dicynodonts of the quadrate and quadrato-jugal to each other, to the squamosal, and to the lower jaw, have been so fully dealt with by previous writers (see especially Broom, 1912 *a* and 1912 *b*; Sollas, 1916) and correspond so nearly with those in *Kannemeyeria* that a detailed description is unnecessary.

The wing-like plate of the quadrate and quadrato-jugal in *Kannemeyeria* rests in the usual way in a hollow on the anterior face of that part of the squamosal which is drawn down behind them to the articular region. This suspensorial plate of the squamosal has a concave posterior surface, along which in life extended the *depressor mandibuli* muscle.

The glenoid surface is pulley-like, the quadrate forming its inner half, the quadrato-jugal its outer half. These two bones, above the articular surface, are as usual separated by a quadrate foramen. Above this foramen they are separated by a distinct

suture; below the foramen, on the glenoid surface, no suture is visible.

The whole complex rests in the typical manner against the splayed-out distal end of the stout paroccipital process. Between the latter and the quadrate is wedged in the tip of the quadrate ramus of the pterygoid, while on the postero-mesial surface of the articular part of the quadrate is a groove for reception of the outer end of the stapes.

Text-figure 13.
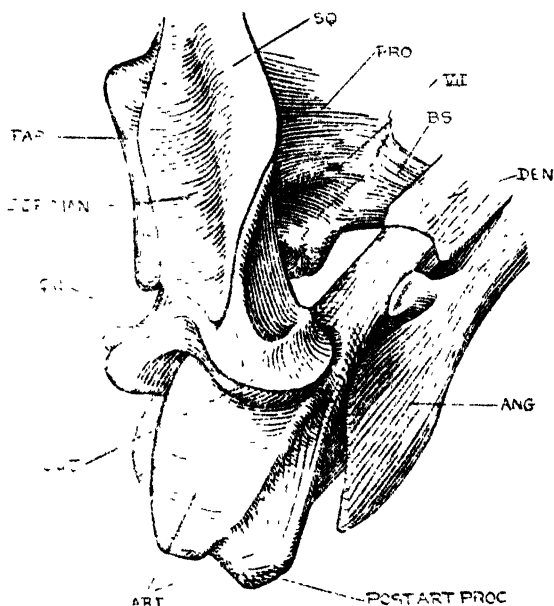
The articular region of the skull of *Kannemeyeria*, viewed obliquely from behind. A composite drawing from various fragments in the British Museum. About one half actual size.

Ang.=Angular.   Art.=Articular.   B.S.=Basisphenoid.   Den.=Dentary.   Dep. Man.=Groove for *depressor mandibuli* muscle.   Par = Paroccipital process. Post.Art.Proc.=Postarticular process of lower jaw.   Pro = Prootic.   Qu.= Quadrate.   Qu.J.=Quadrato-jugal.   Sq.=Squamosal.   VII.=Foramen for facial nerve.

Text-figs. 13 and 14 are two views of the articular region, text-fig. 13 obliquely from behind, text-fig 14 obliquely from in front. They are composite drawings from R. 3739 and from several fragments such as, especially, R. 3751, which shows exceptionally well the quadrate, the quadrato-jugal, and the contiguous parts of the squamosal and paroccipital process. They attempt not only to show the structure of this region, but also to

express pictorially the possibilities of jaw-movement which such
a structure must have afforded the possessor. Other views of the
characteristic condylar surface of the mandible are given in
text-figs. 15, 16, and 17 of the lower jaw.

In text-fig. 13 the mandible is closed, and the most anterior
part of its condylar surface is drawn up against the most
anterior part of the glenoid surface above it. In text-fig. 14 the

Text-figures 14 & 14a.
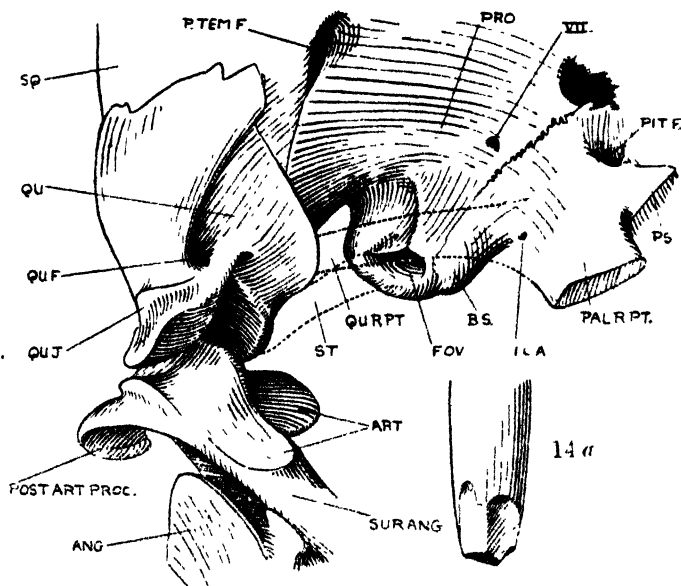
The articular and basipterygoid region of the skull of *Kannemeyeria*, viewed
obliquely from in front. About one half actual size.

F.Ov.=Fenestra ovalis.   I.C.A.=Foramen for internal carotid artery.   P.S.=
   Parasphenoid.   P.Tem.F.=Posterior temporal fenestra.   Pal.R.Pt.=Pala-
   tine ramus of pterygoid.   Pit.F.=Pituitary fossa.   Qu.F.=Quadrate foramen.
   Qu.R.Pt.=Quadrate ramus of pterygoid (dotted outline).   St.=Stapes
   (dotted outline).   Sur.Ang.=Surangular.   Other lettering as in text-fig. 13.

"   14a   Lateral surface of a Dicynodont tusk, showing wear facets.
                     One half actual size.

mandible is widely open (though not quite to the extreme extent
possible), and in opening its crested condylar surface has slid
forwards in the glenoid groove so that now it is their posterior
extremities which are in contact.

With such a joint the mandible, as the Sollas' and Watson
have suggested, could probably also have slid forwards and back-
wards when closed in front, its heavy, grooved anterior end thus

forming a powerful crushing machine with the ridged palatal surface above it.

Text-fig. 13 also shows the post-articular process at the back of the lower jaw for attachment of the *depressor mandibuli* muscles,

Text-figure 15.
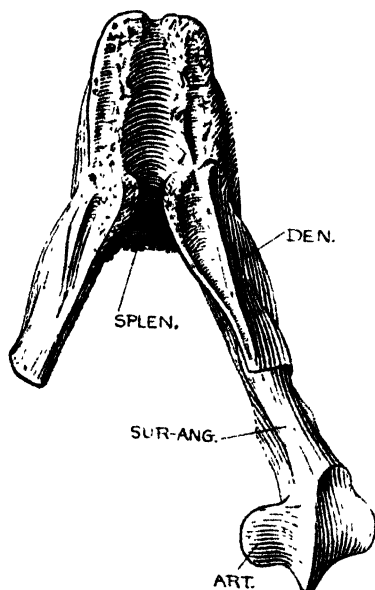
Dorsal view of the lower jaw belonging to the skull of the mounted skeleton of *Kannemeyeria* in the British Museum (Jaw No. 3602, Skull No. 3730). One quarter actual size.

ART.=Articular. DEN.=Dentary. SPLEN.=Splenial. SUR.ANG.=Surangular.

and the well-marked groove on the back of the squamosal, completed by the outer end of the paroccipital process, up which this muscle passed to the top of the skull.

LOWER JAW.

The lower jaw, as stated by Watson in 1912, conforms to the general Dicynodont type. 1 find little new to add to his description, the fullest which has yet been given.

There are numerous fragments of *Kannemeyeria* mandibles in the British Museum. Text-figs. 15, 16, and 17 are of R. 3602, that of the mounted skeleton; this is the most complete, and shows most of the sutures well. That part of the reflected lamina of the angular which projects below the rest of the ramus is

broken off, so that the dotted line representing it in text-fig. 16 is purely arbitrary.

The suture between the articular and the surangular is doubtfully represented on the inner side of the ramus by the anterior edge of the roughened area in front of the articular surface. Between articular and prearticular there is no suture visible, and I have not found one in any of the *Kannemeyeria* specimens ; since it is also lacking in the mandible of the young Dicynodont from Nieuveldt's escarpment, Beaufort West, referred to above, although all other sutures are plainly visible here, this fusion must take place very early in Dicynodonts.

Text-figure 16.
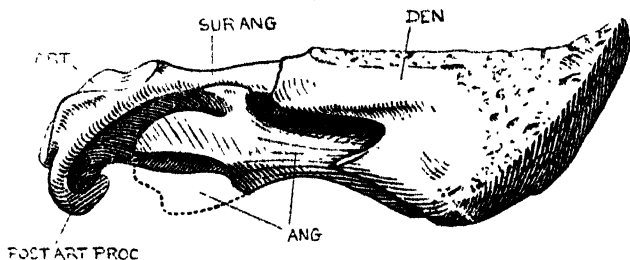
Outer surface of right ramus of jaw No. 3602.   One quarter actual size.

Text-figure 17.
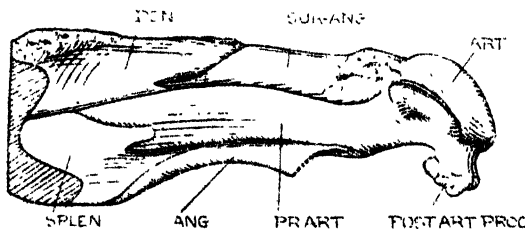
Mesial surface of the above.   One quarter actual size.

Ang.=Angular.   Art.=Articular.   Den.=Dentary.   Post.Art.Proc.=Postarticular process of articular.   Pr.Art.=Prearticular.   Splen.=Splenial.   Sur. Surangular.

The suture between the articular and the angular is well shown ; it is rather further forwards than is usual and partially covered by the reflected lamina.   In no case have I found any evidence of the coronoid referred to by Watson, and I am fairly certain that it does not exist in any of the *Kannemeyeria* material I have examined, nor do I find any trace of it in the young Dicynodont.

Text-fig. 18 is a transverse section through the left ramus of a *Kannemeyeria* mandible, about an inch behind the place where

the anterior end of the angular is lost to sight between the
splenial and dentary. It is based mainly on the fragmentary
specimen R. 3739 *, but agrees in essentials with a slightly more
posterior break-section of R. 3602. It shows the great forward
extension of the surangular, angular, and prearticular within the
dentary and splenial. It also gives examples of the way in
which the jaws are strengthened by their elements being knit
together, the extremity of one bone being wedged into a cleft in
the adjoining bone. Thus, as is also shown in text-fig. 18, the
anterior end of the prearticular is received into a cleft in the
splenial ; a thin lamina of the latter partially covers the outer
surface of the prearticular, and is continuous in front of that

Text-figure 18.
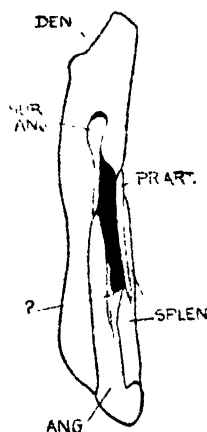
A break-section of the *Kannemeyeria* jaw B.M. No. "3739." The section passes
about an inch behind the place where the anterior end of the angular is lost
to sight between the splenial and dentary (see text-figs. 16 & 17). One half
actual size. Lettering as in text-figs. 16 & 17.

bone, and below its thin ventral edge, with the main body of the
splenial, which itself reaches up a short way on the inner surface.
The splenial itself undergoes a similar process of knitting with
the angular, and the surangular with the dentary. The splitting
into laminæ which results from this sometimes makes it difficult
to identify the bones in cross-section, and I am still uncertain of
the small piece of bone that is shown in text-fig. 18 wedged into
the dorso-mesial surface of the angular ; it thins out entirely
about an inch more posteriorly, and may represent an independent
element entirely concealed from the exterior.

* Although this has the same number as the skull of the mounted skeleton, they
are not really associated. The mandible R. 3602 belongs to that skull, as already
stated.

Conclusion.

In tracing the trend of evolution throughout the group of Theriodont reptiles, Watson [1921] has recognised certain characters as primitive for that group, others as advanced. Apart from their own unique peculiarities, the Dicynodonts as a whole stand out as retaining many of those characters which are primitive, while they have many others of an intermediate nature. Primitive are the large *fenestræ ovales* at the extremity of well-developed basisphenoidal tubera; the exclusion of the parietals from the borders of the temporal fossæ by the meeting of squamosals and postorbitals on their lateral faces; the massive basisphenoids forming a sloping floor to the posterior part of the brain case and continued forwards by a long parasphenoid with a channel on its dorsal surface for the ethmoid to rest in; the slender rod-like epipterygoid; the small size of the brain cavity compared with that of the skull; a *fenestra rotunda* which is merely a notch in the ridge separating the vestibular cavity from the vagal foramen and which thus opens inside the skull; the extension backwards of a quadrate ramus of the pterygoid from the place where that bone articulates with the basisphenoid to the paroccipital process and quadrate: prevomers distinct at least in the young forms; the absence of ridges for turbinal cartilages on the nasals and prefrontals: a nostril directed more laterally than forwards.

Tending in the direction of the changes which Watson has shown to take place in more advanced Theriodonts are: (1) an occipital condyle no longer formed exclusively by the basioccipital, but shared equally between that bone and the two exoccipitals; (2) the articulation of the pterygoids with the ventral surfaces of the reduced basipterygoid processes by a rigid suture, the pterygoids themselves meeting each other below the basisphenoid by a further median suture and thus concealing the processes in a ventral view of the skull; (3) the reduction of the quadrate ramus of the pterygoid from a vertical sheet to a slender bar; (4) an epipterygoid, in some cases at any rate, with a slender quadrate ramus passing backwards from its ventral end along the upper edge of the quadrate ramus of the pterygoid, but not reaching the quadrate bone; (5) a shallow pit, at any rate in the later forms, in a position indicating the beginnings of the definite cochlea canal of more advanced Theriodonts; (6) long and narrow parietals with the parietal (pineal) foramen situated between their anterior ends; (7) the reduction and finally the disappearance of postfrontal bones; (8) prefrontals which are small but which play a part in forming the orbital walls; (9) a maxilla with a deep facial plate which reaches up to the nasal and conceals from without that part of the lachrymal which extends forwards to the septomaxilla; (10) the development of nasopharyngeal ducts and of a rudimentary secondary palate, though in a different manner from that in other Theriodonts.

In the bowing out of the squamosal in order to make more room and more attachment surface for the temporal muscles, the Dicynodonts have gone as far as or further than any other group of Theriodonts, the peculiar structure and the manner of working of their heavy, beak-like jaws calling for the maximum development of this particular trend. Correlated with this, as again shown by Watson in other Theriodont groups, is: (11) the tendency to develop a high, compressed parietal crest; (12) the freeing of the quadrate and quadrato-jugal from their sutural connections with the squamosal and jugal, so that they lie completely within the temporal fossa and acquire a new support by the extension down behind them to the condylar edge of a suspensorial plate; (13) the increased powerfulness of the paroccipital process, which is carried down to the lower surface of the skull and forms a strong additional support to the suspensorial bones; (14) the further enlargement of the temporal fossa by the reduction of the transverse flange of the pterygoid to a small process on the dorsal surface of the bone much anterior to the basipterygoid region.

Kannemeyeria, if it deserves to be placed in a distinct genus, deserves it rather because it has carried to an extreme some of these advances already outlined in Lower Beaufort Dicynodonts, than because it possesses any special peculiarities of its own. Weithofer, in making a new species of *Dicynodon simocephalus* (1888), expressed a similar opinion, and thought that the advances were not sufficient to raise that species to generic rank. He pointed out that the most striking feature of the skull of this type was the great height of its parietal crest and the consequent apparent sinking of its parietal foramen into a deep depression; this, he said, was only an excess of the condition in *Dicynodon pardiceps* and to a lesser degree in many other Dicynodonts. Haughton, in defining the genus *Kannemeyeria* in 1915 and 1917, added but little in the way of distinguishing characters. The oblique angle at which the parietal region is inclined to the frontal plane is a necessary corollary of an extremely high parietal crest; the well-marked depression in which the pineal foramen lies is also due to the bones on either side of it being drawn up to enter the parietal crest behind; the loss of the postfrontal is found already in several Lower Beaufort Dicynodonts, and is probably correlated with the narrowness of the parietal region; skulls with ridged and roughened snouts are also found among Lower Beaufort Dicynodonts; while the breadth of the frontal region is a character highly variable throughout the whole of the Dicynodont group.

It is the same also with most of the other characters of *Kannemeyeria* which Haughton does not list. They are simply a further continuation of tendencies already established in the Dicynodont group when we first know it, and already well developed in many of the larger skulls from the Lower Beaufort

Beds; many of these characters are obviously dependent on each other, while others would very probably prove to be so if we knew more of the habits and mechanical needs of the animal. Adding my own observations to those of previous workers, I would expand Haughton's list as follows:—

1. A parietal crest higher and more compressed than in any other Dicynodont, the sharp angle with which it rises from the frontal plane (highly variable within the genus) causing the pineal foramen to lie in a depression in front of it.

2. The loss of the postfrontal, probably correlated with the narrow parietal region.

3. An occiput deeply sunken between the great wings of the squamosals, which are directed more posteriorly than in any other Dicynodont, thereby increasing the backward extent of the temporal muscles and perhaps also giving a better attachment to the neck muscles.

4. Paroccipital processes directed more downwards than in other Dicynodonts, close to the basisphenoidal tubera. This brings the quadrates nearer together and further below the base of the skull.

5. The backward extension at the expense of the interpterygoid vacuities of that part of the fused prevomers which forms a roof to the nasopharyngeal ducts and a slender vertical partition between those ducts.

6. A great overlapping of the pterygoids and palatines, so that the latter extend back nearly to the basipterygoid region and the former extend forwards to the palatal plate of the maxilla.

7. A great reduction of the transpalatine (ectopterygoid) bone, which has lost all connection with the palatine and jugal, and is a mere rudiment carried far forwards in front of the temporal fossa in the forked anterior end of the pterygoid. This is probably correlated with the reduction of the transverse ramus of the pterygoid in order to increase still more the great temporal fossa. Characters 5 and 6 (given above) may be mechanical contrivances to counteract the weakening of the central region of the skull caused by the forward extension of these fossæ on either side of it—a weakening very undesirable in view of the massive snout which this central region connects with the back of the skull, and in view of the massive anterior end to the mandible working against the snout. Watson has pointed out [1921, p. 74] that the fusion of the pterygoids and parasphenoid in other Theriodonts into a massive ridged girder, and the loss in them of the primitive type of basipterygoid articulation, must add greatly to the strength and rigidity of the skull; in Dicynodonts the fusion of the pterygoids and parasphenoid does not extend further forwards than the basipterygoid region, so that the conditions in *Kannemeyeria* may be an alternative way of producing the same result.

§ 8. In *Kannemeyeria* the palatal surface of the basipterygoid

region, where the two pterygoids meet each other in median suture behind the interpterygoid vacuity, is concave instead of strongly ridged as in *Endothiodon* and such primitive *Dicynodon* palates as I have seen. How far this is a constant or significant character I am not clear.

9. The forward extension of the zygomatic bar of the squamosal nearly to the front of the orbit and the backward extension beneath the orbit of the zygomatic bar of the maxilla, so that they overlap not only the jugal but each other. This is probably also a strengthening process, and is found in others of the large Dicynodonts (e. g. *Eocyclops longus* Broom, 1913).

10. The presence of a pit for the housing of a small cochlea outgrowth from the inner ear. Broom and the Sollas' have not found any trace of a cochlea in the earlier Dicynodonts of which they examined the auditory region, but this region is known in too few skulls to say that the presence of a cochlea is peculiar to the later types.

11. Skull bones with surfaces much roughened and grooved, not only on the margins of the jaws but on top of the snout, on the supraorbital borders, and on the postorbital bars.

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N.B.—References to the work of earlier writers, such as Owen, Cope, Huxley, Lydekker, and others who published before 1913 and are not directly referred to in this paper, may be found in the paper of that date by Sollas and Sollas in the Phil. Trans.

36. A Dicynodont Reptile Reconstructed.
By HELGA S. PEARSON, M.Sc., F.Z.S.

(Text-figures 19–39.)

INTRODUCTORY.

The history of the earlier finds and descriptions of Dicynodont reptiles has been retold more than once by successive investigators. Seeley, for instance, in 1889 summarized the work of Owen, Huxley, and Cope, and, working over the material originally described by Owen, was able to see in it much more than Owen and to bring the descriptions into harmony with all that had been learnt about fossil reptiles in the interval.

Of Dicynodont skulls Owen's supply had been plentiful and good, but of the rest of the skeleton he had only fragments often poorly preserved. The very few suggestions, therefore, that he did make as to the nature of Dicynodont reptiles have been much modified by material found more recently. He thought that *Dicynodon* was carnivorous, using its great tusks for piercing its prey. Yet the toothless "Udenodont" forms were well known to him, and their skull has all the same specializations in relation to the action of the beak-like jaws that he lays stress on in *Dicynodon*; for instance, the wide span of the zygomatic arch, giving a broad temporal fossa, the great length of this fossa due to the extension backward of the lateral part of the occiput (indicating the powerful action of the temporal and masseter muscles), the powerful muscular attachments afforded by the occiput itself, and the peculiar joint between the mandible and quadrate [Owen, 1876, pp. 34, 37]. The possibility that these toothless forms were females, suggested by Owen himself even at that date and later made practically certain by Broom and Watson [see Broom, 1912], would still exclude such use of the tusks in the everyday life of the animal.

Had Owen had sufficient material to make a complete reconstruction of the skeleton, he would probably have abandoned the idea that *Dicynodon* made active use of the tusks in securing prey. Indeed, he himself warns us, after pointing out the mammalian characters of the pelvis with its six sacral vertebræ, not to infer more from this than that "a heavy trunk was in part supported on a pair of huge hind limbs, and the weight thereupon transferred by a larger proportion of the vertebral column in the

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Dicynodon than in the prone, crawling crocodiles and lizards of the present day " [Owen, 1862, p. 465]*. The portrait of *Dicynodon* that this suggests, lumbering along on its huge limbs with its heavy body not far removed from the ground, is borne out by our further knowledge of the limb girdles, the limbs, the vertebræ, and the ribs, and fits but ill with the conception of predatory habits such as those of a lithe-bodied modern Carnivore.

Owen attempted no reconstruction, but Seeley in 1888 reconstructed a very much crushed and badly-preserved skeleton of a small Dicynodont called by him *Keirognathus cordylus*. Its skull was no more than ten centimetres long, and, according to Broom, it was probably only a young *Dicynodon* [Broom, 1901]. Seeley himself admitted his material to be poor, and offered the restoration with diffidence. As it stands, it certainly cannot be accepted as giving any real picture of the animal. Better material shows that the relation of the shoulder girdle to the body and of the limbs to the limb girdles are quite impossible if the animal is to be articulated at all. The proportions of the limbs to the trunk, described by him as resembling those of a "short-tailed Salamander or Seal rather than those of a Dinosaur or long-limbed Mammal," may be taken as equally unreliable.

After Owen and Seeley the next important contributor to our knowledge of the Dicynodont skeleton has been Broom. Like Seeley he has been concerned less with the appearance of the animal as a whole and the function of the parts, than with the details of structure and the problems of relationship and descent arising from these. The absence of any attempt to deduce the life habits of extinct types by studying those alive to-day is apparent in his description of *Endothiodon bathystoma*, a Dicynodont reptile of which he gave a reconstruction of the whole skeleton in 1905. As to how he arrived at the configuration given in his plate xiv. he gives no explanation, but here again, as in Seeley's drawing of *Keirognathus*, the humerus and femur are standing in a position in which no Dicynodont humerus and femur that I have seen could remain naturally articulated.

Earlier than this, in 1901, Broom gave an account of the skull and skeleton of a Dicynodont, which he then called *Udenodon gracilis*, but has since referred to *Emydopsis trigoniceps*, a form with small molar teeth [Broom, 1921]. This account also could be only moderately complete, as the bones were flattened and only partially freed from the two slabs of rock in which they lay. Gaps are filled in from the bones of other species, however, and it is the first attempt at complete description of the manus and pes of a Dicynodont, though that of the pes he has since declared incorrect. He attempted no reconstruction of the skeleton as

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* Prof. Watson points out to me, however, that the pelvis which Owen refers to " *Dicynodon tigriceps* " in this paper is really that of a Pariasaur.

a whole at that time, but in 1905, in his chapter on "The Reptiles of the Karroo Formation" in Rogers' and Du Toit's 'Introduction to the Geology of Cape Colony,' there appears a figure of "*Udenodon*" reconstructed. Again it is accompanied by no account of those characters, such as the shape and position of articular surfaces, which determine the relation of bones to one another in a naturally articulated skeleton, nor can they be found in his drawings.

Most of the more recent work of Broom on Dicynodonts has been entirely systematic, and concerned with the differentiation of species from the enormous variety of skulls which have been found. In this he has been followed by Haughton in a series of papers published in the 'Annals of the South African Museum.'

Of attempts to reconstruct *Dicynodon* there remains to be mentioned, I think, only one other—that of Watson in 1917. His paper, as its title states, is primarily concerned with the shoulder girdle and fore limb, but it seeks to deduce from this and other evidence the way in which the complete animal must have walked and held itself in walking. Attention is also paid to the mechanics of structure and movement, which the comparative anatomists of the nineteenth century were not concerned with.

Watson concluded that the shoulder girdle of *Dicynodon* must be placed with the upper end of the scapula thrown forwards as in Monotremes, that the humerus projected more or less at a right angle to the body, and that the fore arm was at right angles to the humerus and came down to the ground at an angle of about forty-five degrees. The limited possibility of movement of these bones on one another would suggest, he concluded, ". . . that the fore foot never actually lay below the animal's body and that as a measure for increasing the stability the hind foot of the opposite side was in its most advanced position when the fore foot was retired. The order of putting down the feet would be: left fore, left hind, right fore, right hind. Consideration of these possibilities suggests that the track was wide and the stride fairly long." In support of these conclusions, he refers to the footprint tracks from the Cutties Hillock and Cummingstone Beds near Elgin, which he believes to be probably Dicynodont because of their association (in the Cutties Hillock beds) with the Dicynodonts *Gordonia* and *Geikia*.

Besides his drawing of the reconstructed shoulder girdle and fore arm of *Dicynodon halli* in this paper (text-fig. 34), Watson also figures the humerus and parts of the shoulder girdle of the large South African Dicynodont genus *Kannemeyeria* from the Upper Beaufort Beds (*Cynognathus* zone). As he states, there is some good material of this genus in the British Museum, and sufficient of one individual to provide a mounted skeleton in the exhibition gallery. He therefore suggested to me that,

Text-figure 19.
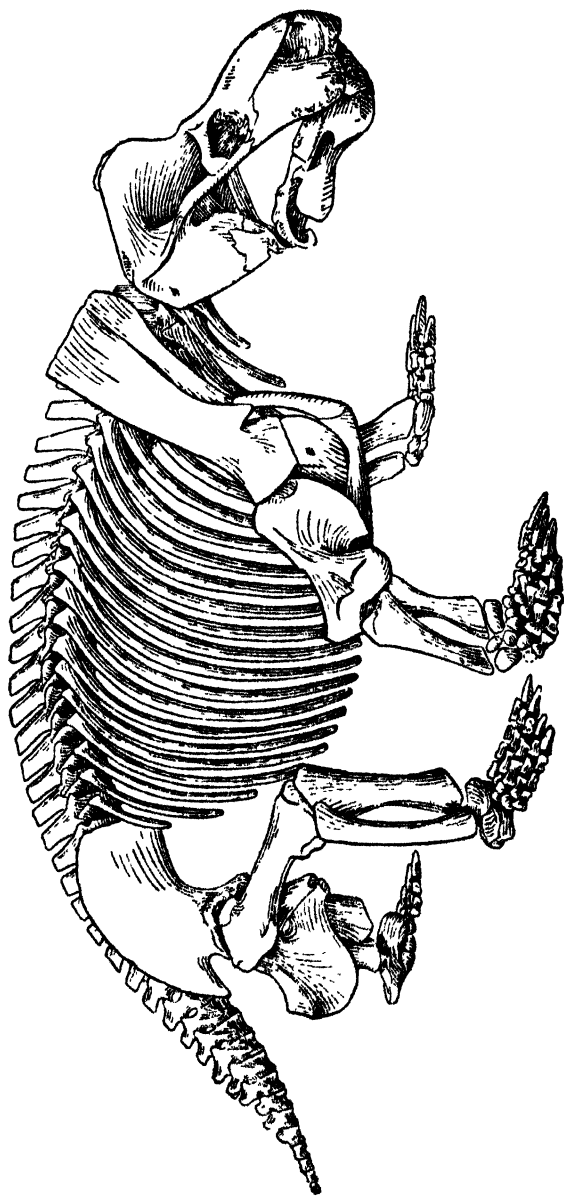
Reconstruction of *Kannemeyeria* from the mounted skeleton and other fragments in the British Museum of Natural History. The bones are all one twelfth the size of those of the mounted skeleton. The clavicle, interclavicle, tibia, hind foot, and end of tail are drawn from Dicynodont material other than *Kannemeyeria*.

considering how few are the accounts of Dicynodont reptiles with good skulls and good skeletons associated, it would be worth while to figure and describe the bones of this genus and to attempt a reconstruction of the skeleton.

The material, though good compared with that of most South African Dicynodonts, is very far from being complete, and some of it is considerably crushed. I put the skeleton together on the evidence of its parts alone, and had very little conception as to what it would look like as a whole until I had drawn those parts in what seemed to be their most probable, or in some cases their only possible, relation to one another. I therefore feel somewhat dubious whether the beast which thus sprung, as it were, into being, ever really walked the earth in that shape. He will serve, however, as a target for criticism out of which may grow a more truthful beast in the future.

Meanwhile I should like to acknowledge my indebtedness to Prof. D. M. S. Watson, under whose guidance I began this work, for all the use which I have made of his experience and material. The use which I have made of his published papers will appear in the sequel.

To the late Dr. C. W. Andrews I am also deeply indebted for his many kindnesses in supplying me with what I needed of the material in his care at the British Museum.

The Reconstruction of *Kannemeyeria*.

The drawing of the reconstructed *Kannemeyeria* given in text-fig. 19 is one twelfth the actual size of the skeleton. Most of the bones represented in it, including the skull, are from the skeleton No. 3592, which is mounted in the fossil reptile hall. But I have straightened these out and filled in gaps with the help of a medley of fragments of other individuals. The drawing therefore represents the genus *Kannemeyeria*, but no particular species of that genus. All parts, however, are drawn to the scale of the mounted skeleton.

Skull.

The skull I have described in detail in another paper. Here it will suffice to say that it is an extreme of Dicynodont specialisation in the height and narrowness of its parietal crest, the downward extension below the cranium of the suspensorial plate of the squamosal, and in the consequent width of gape. With its knob-like condyle it could turn fairly freely on the atlas, but I have drawn it with the floor of the back of the brain-case nearly horizontal. In reconstructing the skull, enough allowance has probably not been made for the crushing backwards of the big plate of the squamosal, which forms the lateral part of the tremendous occiput. If it stood out rather more laterally more of the third cervical vertebra, whose spine and rib alone appear, would be seen, and perhaps also part of the axis-atlas.

Shoulder girdle.

The shoulder girdle is that of which Watson figured the scapula and cleithrum in his paper on "The Evolution of the Tetrapod Shoulder-girdle and Fore-limb" (fig. 18 B & C). His drawings are not four-ninths the actual size as stated there, but rather less than one-fifth. There is a coracoid belonging to this shoulder girdle, and I have also made use of some fragments of another individual (text-figs. 20 and 21 of this paper; fig. 18 A of Watson's) in reconstructing the precoracoid and the broken acromion and glenoid region of the scapula.

Text-figures 20 and 21.
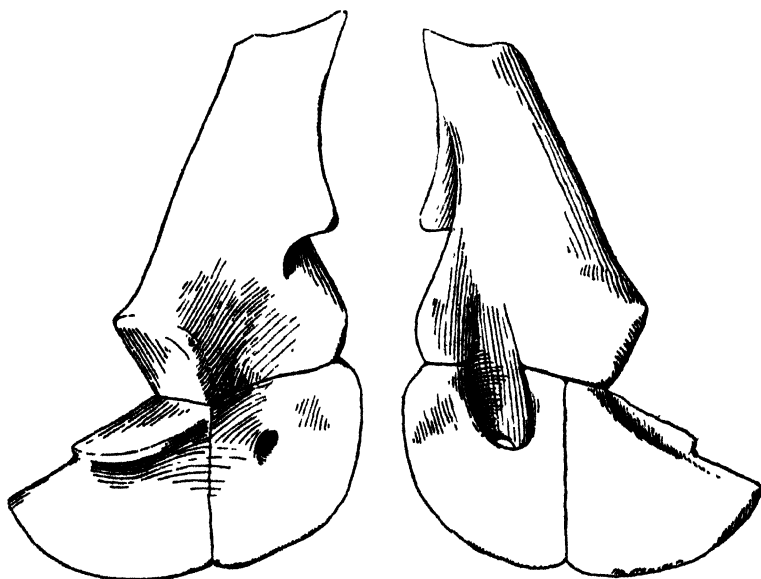
Right shoulder girdle with broken scapula blade. No. 3762 *a*. One quarter actual size. Coracoid reconstructed from left side.

Right shoulder girdle with broken scapula blade. No. 3762 *a*. Inner surface. One quarter actual size. Coracoid reconstructed from left side.

Text-fig. 22 is an anterior view of the scapula, showing on the inner surface of the bone the broad groove for the supraspinatous muscle which leads down under the acromion to the outer surface; above this it shows the groove in the anterior edge of the scapula into which fitted the posterior edge of the splint-like cleithrum. It was only the lower half of the cleithrum which fitted into a groove in this way: further up this groove disappears, and the scapula edge in its turn fits into a groove on the edge of

the cleithrum. The articular face at the lower end of the scapula in front of the glenoid region is for the precoracoid.

The rest of the shoulder girdle pictured in the reconstruction had to be taken almost entirely from small Dicynodonts. There is no clavicle of *Kannemeyeria* in the British Museum, and there is only one very much broken and contorted interclavicle.

Text-figure 22.
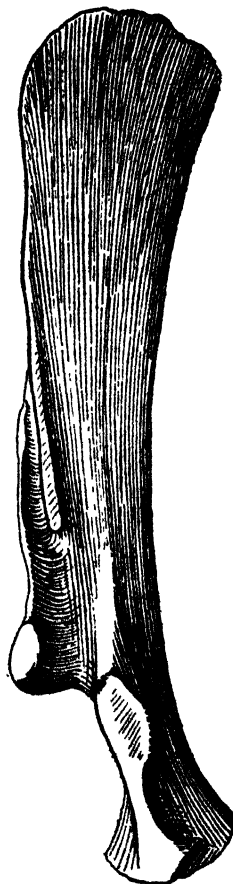
Right scapula of mounted skeleton from in front. No. 3740. One quarter actual size. Precoracoid border partially reconstructed from No. 3762 a.

As regards the forward tilt of the shoulder girdle, it seems, as Watson says in the paper already quoted, that "it is quite impossible to place these bones in any other position so as to give

a possible form to the animal's neck and thorax." Nevertheless, I have not found it necessary to make the tilt quite so great as he did in *Dicynodon halli*. This is because the shoulder blade of *Kannemeyeria*, though longer in comparison with its breadth and with the size of the precoracoid, is not so strongly curved as in the latter; this again, however, may be partially due to the bone in *Kannemeyeria* having been crushed flatter. I have placed, as he did, the coraco-precoracoid border horizontal, and have made the scapula conceal the sixth to the eighth vertebræ and parts of the fifth and ninth.

The exact height of the scapula in relation to the vertebral column cannot be very definitely determined. Its position is closely linked up with the curvature of the neck and back. With this as I have made it, the scapula could not be much higher because of the very long cervical ribs, and it could not be much lower without disturbing the relations of the fore and hind limbs. A scapula with its upper edge above the level of the neural spines is to be found in the Monotremes, where indeed it is even more markedly so, the dorsal vertebræ sloping down much more steeply and joining the neck at a much sharper angle. In their case the space between the two blades and above the level of the spines is occupied by those parts of the *trapezius* and *rhomboideus* muscles which, attaching in front to the skull, further back are attached to their fellows of the opposite side only, or in the words of Mackay [1894] to a "median tendinous raphe."

The extreme arching of the backbone in Monotremes goes with their burrowing habits. The same may be seen in Talpid and Marsupial moles, and these again have an elongated scapula blade reaching above the backbone level. On the habits of *Kannemeyeria* we can only speculate, but although we can hardly think of so big an animal as a burrower, yet the structure of its feet, and their similarity to those of *Echidna*, certainly suggest that it used its fore feet for digging and scraping, perhaps for its food.

Backbone and Ribs.

More reliable evidence should perhaps be gained from the shape of the vertebræ. Unfortunately, very few of these are preserved in the mounted skeleton, and there is now no indication of their order. A study of them, however, together with the very much weathered and crushed vertebral column of another individual (B.M. 3741), complete and in sequence to the twenty-first presacral vertebra, and with skeletons of recent animals, leads to the following conclusions.

The middle cervical vertebræ had comparatively slender, upright spines. Text-fig. 23 represents one of these. The fifth vertebra of the crushed column has sufficient of its neural spine preserved to prove definitely that it was of this type. By the time the eighth or ninth vertebra is reached the spines have

begun to slope backwards considerably, and are becoming broader (text-fig. 24). From this region back to the sacrum the sloping backwards and the broadening of the spines becomes progressively more marked, the spines at the same time shortening and the centra slightly enlarging. Text-fig. 25 is of a mid-dorsal vertebra somewhere in the region of the seventeenth or eighteenth.

This appears to agree with Haughton's statement [1915, p. 97] that, in the specimen he there describes as *K. crithrea*, "the neural spines from the ninth bend backwards and gradually decrease in size" (*i. e.* in height).

Text-figure 23.
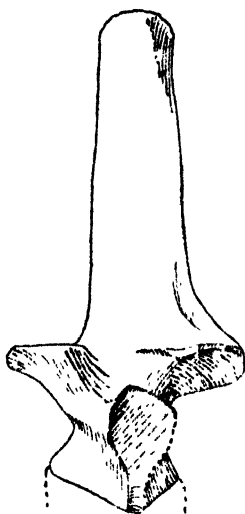
Neural arch of (?) 5th cervical vertebra of mounted skeleton. One half actual size. Transverse process reconstructed from 5th vertebra of No. 3741.

From articulating actual vertebræ of the type drawn in text-fig. 25, I think there can be no doubt, both from the distance between the anterior and posterior zygapophyses and from the shape of the articular faces of these zygapophyses (not well shown in the drawing), that the backbone in this mid-dorsal region must have had a very decided arch upwards.

Besides the characters of the neural spines, those of the transverse processes and ribs have been of use in arranging the vertebræ. It is well known that in Dicynodonts the anterior ribs have forked heads, that the upper prong of the fork articulates with the transverse process of the vertebra, and that the lower prong articulates with a facet on the side of the centrum towards its anterior edge. Also that, in passing from the anterior

cervical region backwards, the two prongs gradually draw together
and finally are fused into a single broad head, the facet on the
transverse process of the vertebra becoming continuous with that
on the centrum, which moves up towards it until the two
together form a long slanting ridge (as in text-fig. 24). Further
back the head of the rib becomes less and less broad, and the facet
for it becomes correspondingly shorter and shorter, the upper
part of the transverse process becoming free from it as in
text-fig. 25.

In the crushed vertebral column of *Kannemeyeria* the first rib
which shows no signs of forking is attached to the seventh

Text-figure 24.
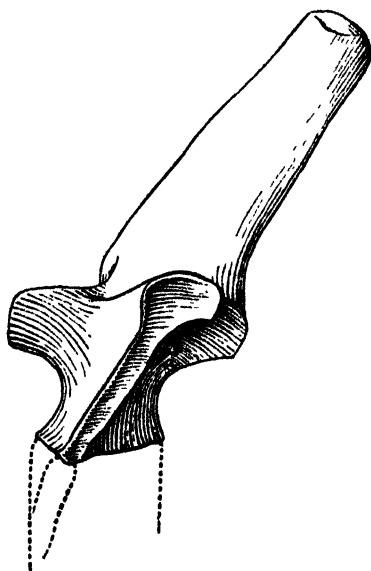
An anterior dorsal vertebra (8th or 9th presacral ?) of mounted skeleton.
One half actual size.

vertebra. It has a head like that represented in text-fig. 26, C,
which is of one of the numerous ribs and rib fragments associated
with the mounted skeleton, and which articulates well with what
I have supposed to be an anterior dorsal vertebra of that skeleton
(text-fig. 24).

The fifth vertebra of the crushed skeleton, with an upright
neural spine, has attached to it a rib-head of the type represented
in text-fig. 26, B. This, then, is a typical cervical rib. The fork-
ing is not nearly so long or so wide as in the smaller and earlier
Dicynodonts. Like all the ribs from the mounted skeleton it is

crushed rather flat, which makes the head have a greater dorso-ventral width than it had in life. Its length is almost as great as that of the anterior dorsals, so that it must have reached down within the shoulder girdle almost as far as the interclavicle.

The thickness and powerfulness of these posterior cervical and anterior dorsal ribs may have been for giving origin to strong *serratus* and *levator scapulæ* muscles, which, inserting above on the inner surface of the top of the scapula blade, would have given that "underslung" condition of the thorax suggested by Romer in his paper on "The Locomotor Apparatus of certain Primitive and Mammal-like Reptiles" [1922, p. 544*].

Text-figure 25.
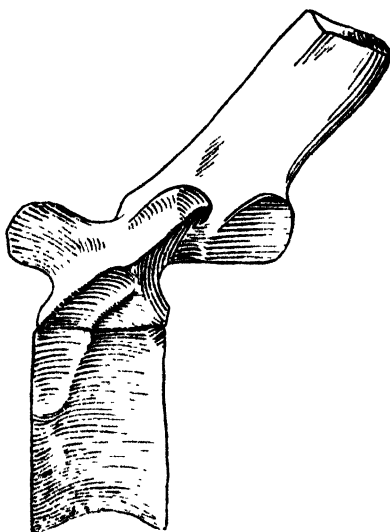
A median dorsal vertebra (17th or 18th presacral ?) of mounted skeleton.
One half actual size.

That there were free cervical ribs as far forward as the axis vertebra is shown by the presence of a facet on the centrum of that vertebra (text-fig. 27). Text-fig. 26, A, is a complete drawing of a small rib which I have taken to be the first of the cervical series because of its small size and the good fit which it makes with the axis.

As regards the hinder end of the vertebral column, there is not so much evidence. In the crushed skeleton there is a gap

* Romer explains the great development of the scapula blade in primitive reptiles by the need for supporting the heavy body above the ground being fulfilled by the muscles of the *serratus* series, instead of by a fusion of girdle with vertebral column as has happened posteriorly in the pelvic region. A dorsal growth of the scapula, he points out, would give a longer play for these muscles.

between the twenty-first presacral vertebra and the sacrum itself.
Of the mounted skeleton there are ten neural arches (they mostly
have centra glued onto them, but these are sometimes back to
front and not necessarily associated). One of these is the
upright cervical of text-fig. 23, one is the anterior dorsal of text-
fig. 24, and the remaining eight, some of them very badly crushed,
appear to be all very close together and from the mid-dorsal
region. There is nothing that seems fitted to support a rib-head

Text-figure 26.
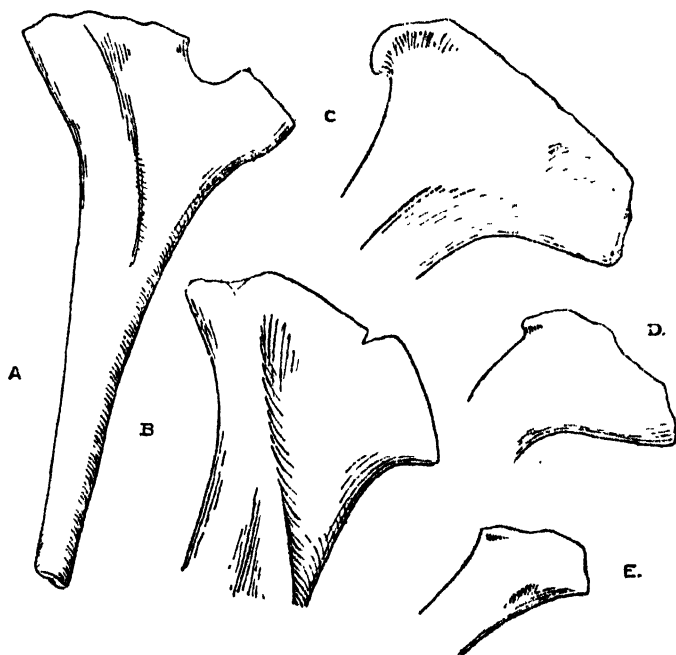
Ribs of mounted skeleton.   No. 3755.   One half actual size.

A. ? First rib, articulating with axis.
B. Head of rib articulating with ? 5th vertebra.
C.   „   „   „   „   anterior dorsal vertebra.
D.   „   „   „   „   median   „   „
E.   „   „   „   „   posterior   „   „

as small as that in text-fig. 26, E, although there are several rib-
heads of about that size or intermediate between that and the
one in text-fig. 26, D.   All of these posterior dorsal ribs, when
complete, are quite long; the shorter ribs that I have attached
to the twenty-second to the twenty-fourth vertebræ in the recon-
struction are conjectural, but I have assumed that they really
were present because rib-heads are attached to all except the last

of the presacral vertebræ in the big Dicynodont (No. 50121) which Owen called "*Platypodosaurus robustus.*"

For the exact number of presacral vertebræ in *Kannemeyeria* I have thus no direct evidence. In Haughton's *K. erithrea* the backbone was only complete to the twentieth. In "*Udenodon gracilis*" Broom guessed that there were twenty-seven. In *Lystrosaurus latirostris* Watson found twenty-five [1912]. Twenty-five is also the number given by Haughton for *Prolystrosaurus natalensis* in his catalogue of the Anomodontia [1917, p. 169]. In the Monotremes there are usually twenty-six, but the number is variable. I have reconstructed *Kannemeyeria* with twenty-five (though admitting that there may well have been another one), the twenty-fifth itself being partially overlapped by the anterior end of the ilium.

The curvature of the ribs, and the position in which they stand when best articulated with the vertebræ, leaves no doubt but that *Kannemeyeria* was a very barrel-bodied beast indeed. In this again, as in the arched backbone and the high shoulder-blade, it resembles the Monotremes and mole-like animals. The Monotremes are so barrel-bodied and so little raised from the ground by their legs that a highly-arched backbone seems necessary to make room for the body at all, and the same appears to have been true of *Kannemeyeria*.

Of the tail of *Kannemeyeria* there is practically no material. One complete caudal vertebra and the centra of two others are associated with the mounted skeleton. There is also a series of six consecutive centra from another individual. Of these latter the first is large enough to have been not far behind the last sacral, and the remainder rapidly diminish in size, but there is no real evidence as to their exact position, and the neural arches are broken. It is evident that the tail must have been short, as Broom also found in "*Udenodon gracilis,*" but the number twelve that I have given in the reconstruction is entirely arbitrary; it is the number which Watson suggests for *Lystrosaurus.*

Of sacral vertebræ *Kannemeyeria* had almost certainly six, the same number as Owen found in *Dicynodon tigriceps* and Watson in *Lystrosaurus.*

Pelvis.

In the pelvic girdle (text-fig. 29) the bones are less thick and massive in proportion to their size than in more typical Dicynodonts, and the ilium is more expanded and plate-like. In this expansion it resembles the girdle of *Cynognathus*, except that the post-sacral extension backwards alongside the tail is comparatively short. The whole thing is very much like that of *Lystrosaurus*, as figured by Watson [1912], but the dorsal border of the ilium, though slightly irregular in outline, has not the deep indentations of that genus, and the obturator foramen appears to be larger. The anterior edge of the ilium is broken in the mounted skeleton,

Text-figure 27.
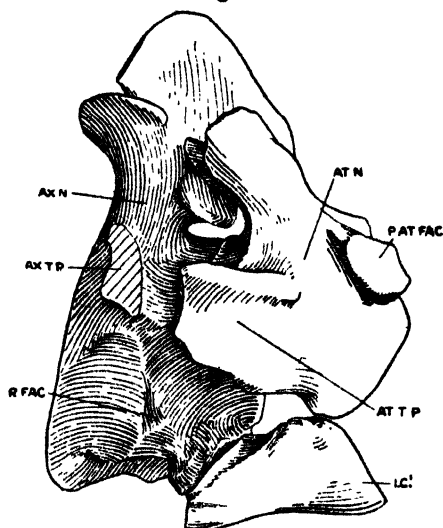
Right side of axis-atlas of mounted skeleton. One half actual size.
Partially reconstructed from left side.

At.Fac.= Facet for neural arch of atlas. At.N.=Neural arch of atlas. At.T.P.=
Transverse process of atlas. Ax.N.=Neural arch of axis. Ax.T.P.=Transverse
process of axis (broken.) I.C.[1]=1st intercentrum. P.At.Fac.=Facet for pro-
atlas. R.Fac.=Facet for 1st rib.

Text-figure 28.
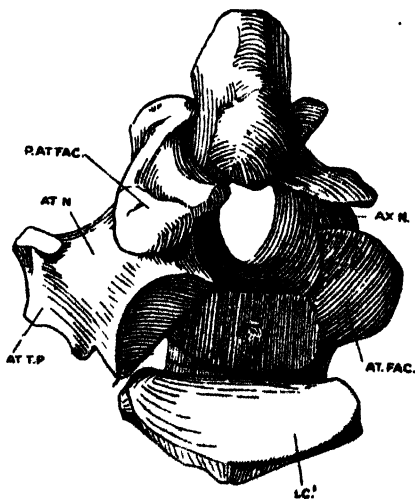
Axis-atlas of mounted skeleton from in front. One half actual size. Left half
of atlantal neural arch missing. Lettering as in text-figure 27.

and I have again reconstructed from the bone of another indi-
vidual (No. 3762 c).   The pubis projects downwards and forwards
from the acetabulum in a strong process which the thinner
ischium, bowed inwards beneath the obturator foramen, meets
below and in front of the latter.   The anterior corner of the
girdle at this point, instead of tapering off to an edge as elsewhere,
is thick and roughened, suggesting that it supported some sort of
cartilaginous epipubis.

Text-figure 29.

Right half of pelvic girdle of mounted skeleton.   One fifth actual size.
Dotted borders of ilium reconstructed from No. 3761.

The pelvis of the mounted skeleton has one very peculiar
feature shared by no other Dicynodont pelvis I have seen[*].
In most Dicynodonts the hinder border of the ischium is a
smoothly-rounded edge, expanded at the back of the acetabulum
above but moderately thin below at the ischial tuberosity.   In
this pelvis it is bent inwards to form a triangular flange that
stands almost at right angles to the general surface of the
bone.

[*] I should judge it to be the pelvis which Jaeckel figures on p. 191 of ' Die
Wirbeltiere ' as the right half of the pelvic girdle of a Dicynodont in the British
Museum.   He makes no further comment.

The plane in which each half of the pelvic girdle lies in relation to the vertebral column is fairly certain, owing to the long line of well-marked sacral articulations along the inner surface of the ilia.   A check to this is the big Dicynodon pelvis (No. 47090) which Owen called "*Platypodosaurus robustus*" [1881], and in which the two halves are articulated with the sacrum and apparently little distorted.   The width of each of the sacral vertebræ is also known approximately.   If, then, the two halves of the girdle are placed in what appears to be their natural position with regard to one another, a condition such as that drawn in text-fig. 30 is the result : the two inwardly-turned ischial flanges approach one another above what must have been the cloacal aperture, but below this there is no pelvic symphysis whatever.

Text-figure 30.
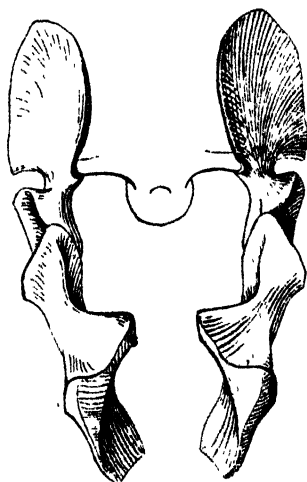
Pelvic girdle of mounted skeleton from behind.

In *Ornithorhynchus* the upper edge of the ischium between the acetabulum and the ischial tuberosity gives origin to a thick muscle which inserts at the proximal end of the femur on the ventral surface of the great trochanter.   Westling [1889] calls the corresponding muscle in *Echidna* "*quadratus femoris*," but I have somewhat carefully compared the monotreme condition with that in *Didelphys*, and find that this muscle has exactly the same relations to those around it, and to the femur and girdle, as the *obturator internus* of the placental, except that it does not extend down onto the inner surface of the ischium, for which reason Westling reported an *obturator internus* to be absent. Arising from the outer surface of the ischio-pubic plate and the obturator region, and inserting on the ventral surface of the

proximal end of the femur, there are in *Ornithorhynchus* two other short, thick muscles. The more anterior of these in *Echidna* Westling calls *obturator intermedius*, the more posterior (bordering on his "*quadratus femoris*") *obturator externus*. These two muscles, which lie beneath the adductors, are clearly homologous with the similarly situated muscle mass called by Gadow in living reptiles the *pubo-ischio-femoralis externus*, and variously subdivided. That the placental *quadratus femoris* is a derivative of the latter and not of the reptilian *ischio-trochantericus*, Romer [1922] has already concluded from its insertion. The rest of the *pubo-ischio-femoralis externus* is represented by the placental *obturator externus*. Thus the two obturator muscles of monotremes probably together represent the *quadratus femoris* and *obturator externus* of placentals. The *obturator internus* of placentals. Romer [1922] and Gregory and Camp [1918] have derived from the reptilian muscle which Gadow calls *pubo-ischio-femoralis posterior* in recent reptiles and Osawa *ischio-trochantericus*. This is a small muscle arising like the placental *obturator internus* from the inner surface of the ischium, though much more posteriorly, and inserting very proximally on the femur. The condition in Monotremes, where there is no femoral muscle extending down within the girdle posterior to the acetabulum, seems to me to raise a doubt as to the homology, and to suggest that the *obturator internus*, like the *quadratus femoris*, is really a derivative of the old reptilian *pubo-ischio-femoralis externus* group. It would be too great a digression to pursue the question here, but it is intimately connected with that of the homologies of the muscles passing posteriorly to the girdle from the tail, a question which needs further investigation making use of the Monotremes as well as of Theriodont bones to suggest a stage intermediate between living reptiles and placental mammals.

My reason for tracing these muscles here at all was to seek the purpose of the curious triangular flanges described above on the ischia of *Kannemeyeria*. I can only suggest that they gave origin to the *obturator internus* muscles, and would thus represent an early attempt to bring that origin from a position on the upper edge of the ischium to one further within the girdle. This would increase the force of their pull on the femur, a pull counteracting that of the gluteals, which, with an insertion on the dorsal surface of the great trochanter, must have taken origin from most of the greatly expanded iliac plate, and therefore been themselves very powerful muscles.

Limbs.

With limb girdles and vertebral column as I have described them, and the typical Dicynodont limb bones represented in textfigs. 31 to 37, *Kannemeyeria* must have held itself in walking very much as Watson pictured *Dicynodon* doing (see above, p. 829).

Watson himself, it is true, held that in *Kannemeyeria* the humerus did not project so strongly from the animal's body, but that even in its most anterior position it was drawn backwards more closely against the flank, as in Cynodonts and other more active forms. This is in agreement with his statement that the glenoid cavity of the *Kannemeyeria* shoulder girdle faces more directly backwards than in smaller and earlier forms. I have not been able to convince myself, however, that there is really any significant difference; if the shoulder girdles are placed

Text-figure 31.
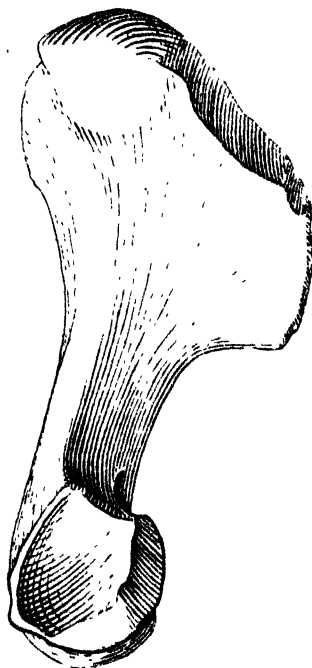
Right humerus of No. 3762 *a* from in front.   One quarter actual size.

in similar positions their glenoid cavities appear to me to be practically similar also, though both undoubtedly facing very much more posteriorly than in earlier Permian forms of other groups.

From the completely uncrushed *Kannemeyeria* humerus No. 3762 *a* (text-figs. 31 & 32), it would further appear that the plane of expansion of the distal end of that bone forms at least as equally great an angle with the plane of expansion of the proximal end as in *D. halli* (an angle of about sixty degrees). This fact is very liable to be obscured by the frequency with

which the bones are crushed so that, as in Watson's fig. 19, the expanded ends are twisted and flattened into nearly the same plane.

The articular surface of the head of the *Kannemeyeria* humerus looks, as in *D. halli*, almost entirely upwards and forwards; it extends also onto the rather thin edge of the proximal end of the bone, resting here, it would appear, on the glenoid surface of the coracoid, but it does not pass onto the postero-ventral surface.

A consideration of the head of the humerus in relation to the glenoid cavity, and of the twist of the humerus in relation to its articulation with the fore arm, leads to the conclusion that the upper arm in *Kannemeyeria*, as in *D. halli*, did project very much to the side; that even in its most posterior position it could not be drawn in at all close to the flank of the animal; and that also as in *D. halli* the humerus, when in its most anterior position, had its distal end raised above the level of its proximal end, while when in its most posterior position its distal end was lowered.

It is this most posterior position in which I have placed the right fore limb of *Kannemeyereria* in the reconstruction. The nearly concealed left fore limb is in a position similar to that in Watson's fig. 16 of *D. halli*. The right fore limb with its fore arm bones flexed backwards and inwards is on the point of being drawn up from the ground and swung forwards again. Meanwhile it has been nearly caught up by the forwardly-extended right hind limb, the pes pressing hard upon the manus.

From the shape of the acetabulum and of the head of the femur it appears that the latter could be drawn in rather nearer to the animal's flank than could the humerus, while it could not have been drawn very far backwards without the great crest of its trochanter hitting against the rim of the acetabulum. Thus the hind limb appears to have advanced further towards the mammalian condition than the fore limb.

Limb bones.

Text-figs 31 and 32 are of the humerus No. 3762 *a*, mentioned above as being a completely uncrushed specimen. It is of the right side and is approximately the same size as those of the mounted skeleton, the left of which is figured by Watson, but the twisting and flattening makes exact comparison difficult. In text-fig. 32 the ectepicondyle, viewed from in front in text-fig. 31 but broken away there as in the actual specimen, is restored from other fragments, the rather large surface for articulation with the radius being shown complete. The articular surface for the ulna partly appears on this same side of the humerus and partly curls round onto the dorsal side, suggesting that the fore arm bones were capable of considerable flexion and extension. In the reconstruction I have represented them as flexed.

Text-fig. 33 is of the medial surface of the left ulna of the mounted skeleton. The corners of the bone are somewhat worn in the original specimen and were in any case doubtless capped by cartilage, but it shows that there was a well-developed olecranon with an articular surface for the humerus extending up its antero-median edge; below this surface is the pit in which lodged the postero-lateral corner of the head of the radius.

Text-figure 32.
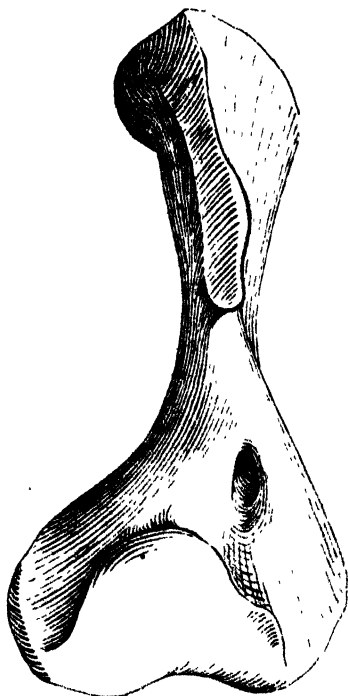
Ventral view of right humerus of No. 3762 a.   One quarter actual size.
Ectepicondyle reconstructed from other fragments.

The mounted skeleton has no radius.   In reconstructing I have used that of another, rather larger, individual (No. 3761) and those from the very much weathered and crushed set of bones (No. 3741) that belong to Seeley's type skull of *Kannemeyeria*— the same set to which belongs the crushed vertebral column already referred to.

There is no complete uncrushed femur in the British Museum, but although the flatness of those of the mounted skeleton (text-figs. 34 & 35) is exaggerated, yet the bone was evidently of the

broad, flat type which we get also in the Monotremes and Deinocephalia. There is no trace of the lesser trochanter of the former, and the crest of the great trochanter is, as in the latter, continuous with the head.

Text-figure 33.
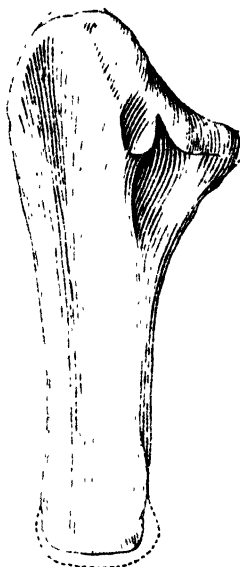
Postero-mesial view of left ulna of mounted skeleton.
One quarter actual size.

A *Kannemeyeria* tibia is entirely lacking, so this bone I have had to reconstruct from other Dicynodont material. The fibula is reversed from that of the left side of the mounted skeleton (text-fig. 36).

Feet.

Of both manus and pes the material is again rather scanty and poor. Text-fig. 37 represents the left manus of No. 3741. The carpal bones are really a reversed drawing of those of the right side; they are obviously displaced from their natural positions, especially the distal row, and all the bones are in the same bad state of preservation as the rest of the type *Kannemeyeria*. The carpus must have been completed by a large proportion of cartilage. The terminal phalanges in the actual specimen are flexed under the proximal ones.

Belonging to the mounted skeleton there are a number of foot bones. These are beautifully preserved and uncrushed, so that in the reconstruction I have drawn, though somewhat diagrammatically, the individual phalanges, metacarpals, and

Text-figures 34 and 35.
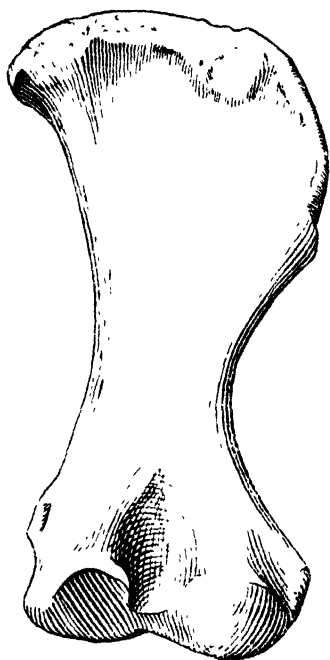
Ventral view of right femur of mounted skeleton.   One quarter actual size.
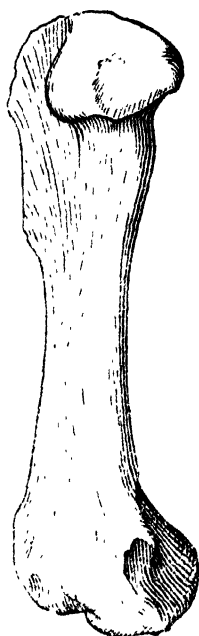
Right femur of mounted skeleton from in front.   One quarter actual size.

Text-figure 36.

Postero-mesial view of left fibula of mounted skeleton.   One quarter actual size.

metatarsals from these rather than from No. 3741. From the
total number of each kind it is evident that hind foot bones are
mixed with fore foot, and in sorting them it becomes clear that
those belonging to the former are much smaller and weaker
than those of the latter. In fact, the digits of the pes were
probably less than three-quarters the length of the digits of the
manus and proportionately less stout. This is much what Broom
found in "*Udenodon gracilis*"; he says: "Though the fore and
hind limbs are fairly equal in length the pes is very much smaller
than the manus. All the digits are much more feeble and the
claws are only about one-third the size of those of the manus."
On this evidence, and on that of one rather large bone which
seems to have been the fibulare, I have ventured to reconstruct

Text-figure 37.
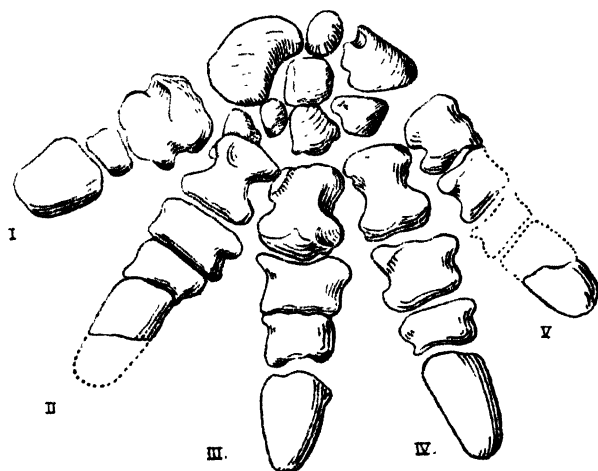
Dorsal surface of left manus of No. 3741.   One quarter actual size.
Carpal bones reversed from those of right side.

the hind foot, making use also of Broom's revised figure of
"*Udenodon gracilis*" (*Emydopsis trigoniceps*, 1921) and of
Watson's paper on "The Limbs of *Lystrosaurus*" [1913 a].

If the bone which I have drawn in text-fig. 38 is really the
fibulare, and by a process of elimination it seems as if it must be.
it is of exceptional interest because it shows an articular facet on
what appears to be its dorsal surface. This would be for the
fibula and probably also the tibia to rest upon, and would mean
that *Kannemeyeria* was in the initial stages of developing a heel
to its hind foot.

In his paper on "The Limbs of *Lystrosaurus*" Watson
describes the first phalanx of the *Lystrosaurus* manus as
"a curious nodule of bone which in longitudinal section is

triangular, the dorsal surface being flat and the articular surfaces nearly meeting below." Further on he says of the manus: "The most curious feature is the triangular section of

Text-figure 38.
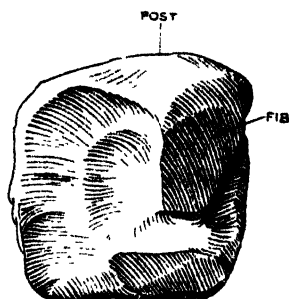
Left (?) fibulare (?) of mounted skeleton. No. 3760, dorsal surface. One half actual size. Post. = Posterior border. Fib. = Facet for fibula.

the first phalanx, which allows of very great flexion of the digits; the same feature occurs in *Kannemeyeria* and in Monotremes, to the foot of which that of Anomodonts offers many resemblances, as Owen, Seeley, and Broom have already recognized."

The articular face at the distal end of the second phalanx in

Text-figure 39.
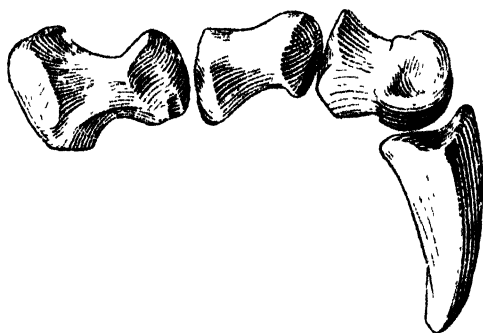
Flexed claw of manus, reconstructed from series of loose foot bones associated with mounted skeleton. No. 3760. One half actual size.

Kannemeyeria is not flat and parallel to that at the proximal end, as Watson reports it to be in *Lystrosaurus*, but curves down onto the ventral surface and extends back on that for about half the length of the bone. This allows the ungual phalanx to be

bent down on it almost at a right angle, thus enormously
increasing the possible flexion of the digit.

Hind and fore feet are alike in these respects.

In text-fig. 39 I have drawn a flexed claw of *Kannemeyeria*,
selecting from the collection of loose foot bones associated with
the mounted skeleton a metacarpal and three phalanges, each the
largest of their kind

Habits and Environment.

Paws such as these are clearly adapted for digging or scraping,
just as are the similarly constructed ones of Monotremes. I
have already pointed out that the build of the rest of the
skeleton is not unlike that of these burrowing forms. If *Kanne-
meyeria* is too big to have burrowed, it may perhaps have scraped
a hole for itself in the ground, but more probable is the view
that it dug to obtain its food. That its tusks were not expressly
intended for digging is clear for the same reasons that they were
not intended for catching active prey ; but that they were really
worn (not just broken) on their ends and outer surfaces may be
seen in such cases as that in text-fig. 14 *a* of my paper on the
skull of *Kannemeyeria* (see above, p. 818), and Watson has
described tusks in *Lystrosaurus* actually truncated at the end
and worn smooth. If the tusks were there and the animal dug
for its food this would inevitably happen.

Watson has hesitated between a plant and a shell-fish diet for
Lystrosaurus, the massiveness of the jaw suggesting something
harder than aquatic plants, the scarcity of shells making shell-
fish also doubtful. Besides the digging claws and the worn
tusks there must not be forgotten the probable horny beak over
the turtle-like jaws and the very wide gape of the mandible,
reaching an extreme in *Kannemeyeria*. The mandibular joint,
moreover, (see text-figs. 13 & 14 in the preceding paper),
indicates that the lower jaw could be slid backwards and forwards
against the upper in crushing the food, and to aid in this there
are ridges on the front of the palate fitting into grooves on the
upper edges of the dentaries.

Dicynodon and *Kannemeyeria* lived on dry land and, as Watson
tells us in another paper [1913 *b*], probably under almost desert
conditions. He compares the Beaufort Beds of South Africa in
which they are found with the Tertiary deposits of the Great
Plains of North America, both of which used to be regarded as
lacustrine. Matthew, Hatcher, and others have shown that the
North American deposits were laid down on flat plains as flood-
plain and river-channel deposits modified by wind-action : they
consist partly of stratified sandstones containing the remains of
forest and river-living animals, partly of fine, unstratified clays
containing skeletons of plains-living types. Watson finds very
similar conditions in the Beaufort Beds, the typical Dicynodonts
and most of the other Karroo reptiles representing the dry-land

has come clean and freely out, leaving the surface to imagination as of a fine and leathery feel. It has been slightly undulated, though not divided into separate pads; but on the hind foot there has been a distinct posterior pad or heel, while the outer portion of the sole seemed to form another large one, all preceded by very slight elevations of the five toes. These pads and elevations appear, of course, as slight hollows in the impressions." (p. 11.)

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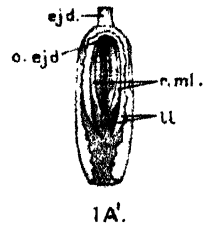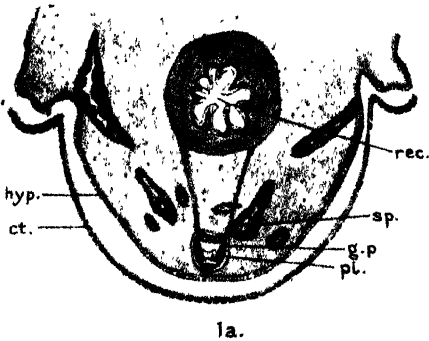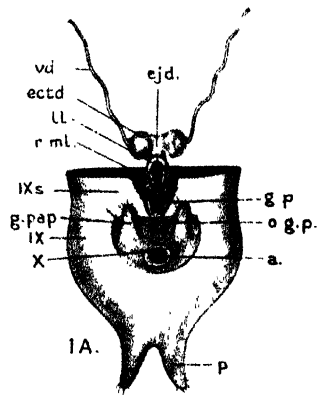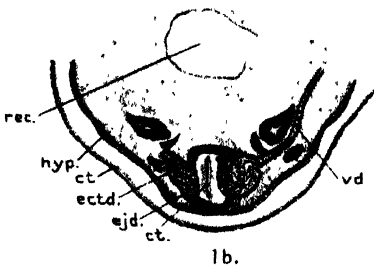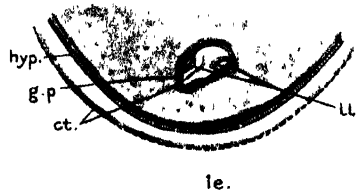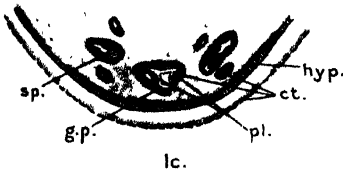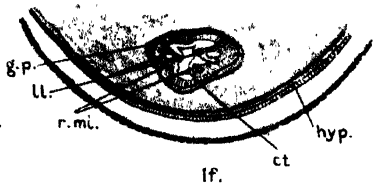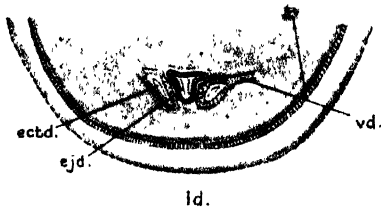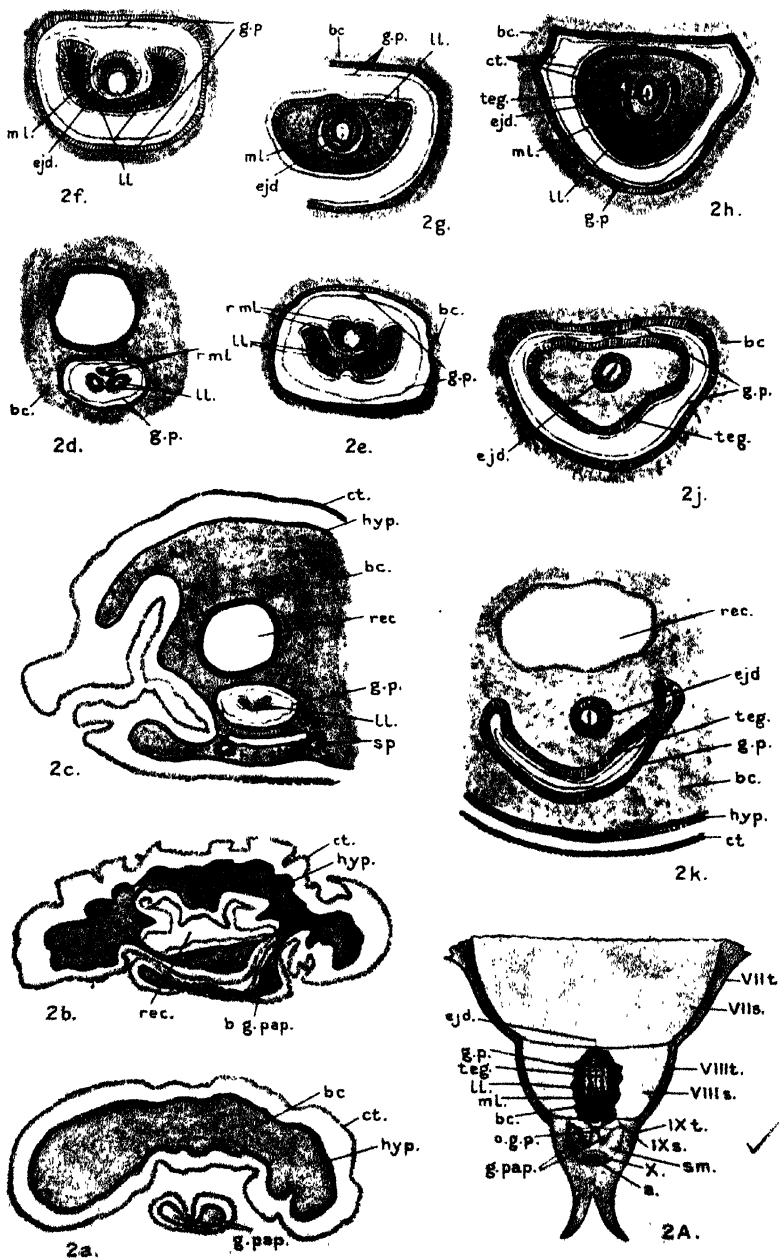
MALE GENITAL ORGANS OF TENEBRIO MOLITOR.
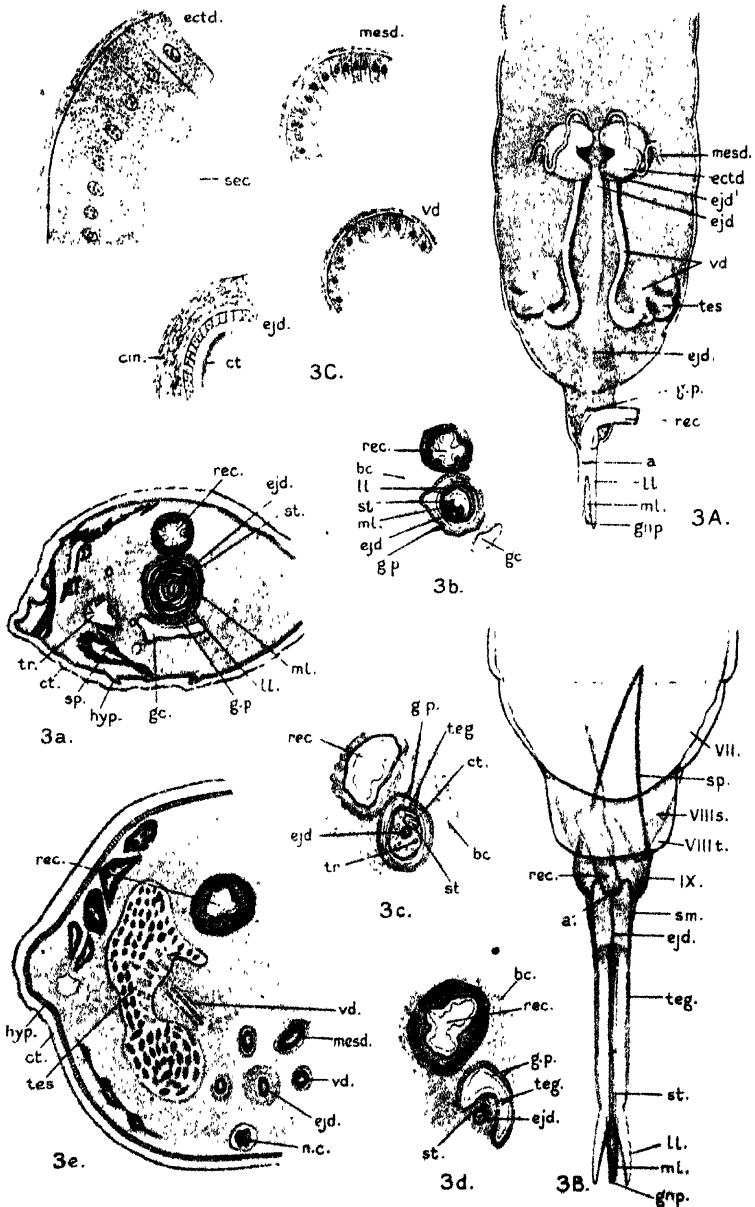
MALE GENITAL ORGANS OF TENEBRIO MOLITOR.

MALE GENITAL ORGANS OF TENEBRIO MOLITOR.

37. On the Post-Embryonic Development and Homologies
of the Male Genital Organs of *Tenebrio molitor* L.
(Coleoptera). By HEM SINGH PRUTHI, M.Sc.
(Punjab) *. (From the Zoological Laboratory,
Cambridge.)

(Plates I. III.†; Text-figures 1–3.)

INTRODUCTION.

Zander (**24 26**), Christophers (**6**), Singh Pruthi (**21**), and
others, while differing in several important points, all came to
the conclusion that the copulatory organ in Insects originates
as a pair of appendages, which subsequently fuse with each
other to form the single tubular organ of the adult. This
general statement could not be applied to the Order Coleoptera,
in which, according to Muir (**12**), almost the only investigator
who has studied the group from this point of view, the "genital
tube," from the very beginning, is a hollow diverticulum, and has
at no stage the appearance of a pair of appendages. Evidently
Muir's conclusions required confirmation or contradiction, and it
was mainly for this purpose that the present investigation was
undertaken. Larvæ and pupæ have been sectioned, and it is
found that the genital organ in this group, as in all other groups
of insects, does originate as a pair of appendages, and even
retains its paired appendage nature till the pupa is three or four
days old. Muir failed to observe this fact, probably because his
study was carried out only by dissections, and he confined
himself to pupæ and did not study the conditions in the larva.

Closely connected with the above is the question whether a
sternite or tergite of a body segment participates in the
formation of the external genital organs. In adult Coleoptera,
as is well known, the posterior abdominal segments, beyond the
eighth, are generally membranous and indistinguishable, and
many authors believe that parts of these posterior segments
are incorporated in the genital armature. Muir suggested the
improbability of such a theory, and my observations on *Tenebrio
molitor* confirm his views.

Then, the whole question of the homologies of the genitalia of
Coleoptera is still *sub judice*—this is especially the case with
regard to the "ultra morphology"—to use Sharp's words—of

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* Communicated by F. BALFOUR BROWNE, M.A., F.Z.S.
† For explanation of the Plates, see p. 867. The lettering of the text-figures and
plate-figures is uniform.

the lateral appendages, the "lateral lobes," "parameres," etc. Much theorizing is associated with these organs, and a final opinion based on strong evidence has not yet been pronounced, with the result that whosoever has attempted the homologies of the lateral appendages of insects in general has done so almost independently of the lateral appendages of Coleoptera.

As regards the internal efferent genital system, there are two series of organs, the mesadenia and the ectadenia (Escherich. **8**), whose nature is under dispute and is of great morphological importance. Escherich believed that while the ectadenia are ectodermal in origin and resemble the ejaculatory duct, the mesadenia are diverticula of the vasa deferentia and are therefore mesodermal structures. Blatter (**1**) confirmed the conclusions of Escherich. Bordas (**2–4**) differed from these authors and concluded that both organs are of mesodermal origin. At present Escherich's view is generally accepted and is incorporated in the text-books. None of these investigators had recourse to ontogenetical evidence. The developmental history of these organs in *Tenebrio molitor* indicates that the conclusions of both Escherich and Bordas require a radical modification.

Of the various systems of terminology in vogue for the genital organs of Coleoptera, that of Sharp and Muir (**19**) has been adopted in the present paper.

It is with great pleasure that I express my feelings of indebtedness to Mr. F. Balfour Browne, M.A., for the keen interest that he showed in my investigations and the valuable suggestions that he made with regard to them.

GENERAL ACCOUNT OF THE ORGANS OF THE IMAGO.

(Pl. III.*)

Figure 3 A illustrates the internal reproductive organs. A pair of testes (*tes*), one on either side of the alimentary canal, lie in the region of the 6th-7th abdominal segments. Each testis is connected to a vas deferens (*vd*), which is thrown into a loop in the proximal region and consequently runs forward. The vasa deferentia, extremely narrow near the testes, are quite wide for the rest of their length. In the region of the 4th or 5th abdominal segment they open into the ejaculatory duct (*ejd*), which is slightly bifurcated at its proximal end, each bifurcation (*ejd¹*) receiving the vas deferens of its side. The mesadenia (*mesd*) and ectadenia (*ectd*) also open into the ejaculatory duct at this point; the mesadenia are simply a pair of convoluted narrow tubes, while the ectadenia are bean-shaped and extremely conspicuous.

In the general histological structure (Pl. III. fig. 3 C), the vasa deferentia, the mesadenia, and the ectadenia are similar to one another, except that the cells lining the latter two are more or

* All the figures on Pl. I. illustrate the organs of the larva, those on Pl. II. of the pupa, and those on Pl. III. of the imago.

less glandular, and moreover those of the ectadenia are very much enlarged and swollen. The ejaculatory duct differs from all these in having an enormously thick coat of circular muscles (*cm*) and a distinct chitinous lining (*ct*).

As regards the external organs (Pl. III. fig. 3 B), a large membranous area (*sm*) intervenes between the eighth sternite and the anus. In the condition of repose this area is invaginated into the body, forming a deep pouch in which the external genital organs lie; the pouch therefore will be henceforward referred to as the genital pocket. The genital organs have the appearance of a highly chitinized long cylinder which is continuous at its base with the genital pocket and is divided at its apex into three lobes, two large lateral lobes (*ll*) and one small median lobe (*ml*). At their bases the lateral lobes are not distinct from each other, they meet in the mid-dorsal and ventral lines and consequently surround the proximal region of the median lobe, better seen in Pl. III. fig. 3 *a*. The long and undivided part of the cylinder is the tegmen (*teg*); it is markedly dechitinized in its dorsal region. Sharp and Muir originally used the term "basal piece" for this region, and included under the name "tegmen" both the "basal piece" and the "lateral lobes." But Muir, in his recent works, has designated this part alone as tegmen, a course which has been followed in this paper.

The long and straight ejaculatory duct (Pl. III. figs. 3 A and 3 B), very wide proximally, narrows in the posterior region of the abdomen, pierces the genital pocket at its bottom, traverses the tegmen, enters the median lobe and ends at its apex at the gonopore (*gup*).

The dorso-lateral regions of the median lobe are thickened into a pair of rod-like organs, the median struts (*st*), which extend anteriorly as far as the base of the tegmen (Pl. III. figs. 3 B & 3 *a*-3 *d*).

The spiculum (Pl. III. fig. 3 B, *sp*) has the form of a heavily chitinized V-shaped structure, the arms of the V lying one on each side of the genital pocket, with their ends in contact with the membranous body-wall behind the eighth segment. It forms a basis for the attachment of powerful muscles (Pl. III. fig. 3 *a*).

DEVELOPMENT.

(a) *External Genital Organs.*

In the larva (Pl. I.) there are nine distinct tergites and sternites in the abdomen; the ninth tergite (fig. 1 A), as compared with the sternite, is very much enlarged with the consequence that the anus, borne by a soft and membranous papilla (? tenth segment), lies on the ventral side instead of at the posterior end of the body. A pair of papilla-like appendages (*g. pap*), to be designated as "genital papillæ," are present at the posterior

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margin of the ninth sternite. Another pair of projections (*p*) lie at the extremity of the body; they are processes of the ninth tergite and are of no importance from our present point of view and therefore they will not be mentioned again. There is an invagination of the body-wall just behind the ninth sternite (*g.p*); this is the beginning of the genital pocket; the latter is of a very small diameter at this stage, and its mouth or opening (*o.g.p*), also very minute, resembling the anus in appearance, lies between the bases of the genital papillæ, in the mid-ventral line. ·

The genital pocket, otherwise quite thin-walled, is thickened at its bottom, especially in its lateral regions (Pl. I. fig. 1 *a*). When the larva is almost fully grown, the lateral thickenings become very conspicuous, project into the lumen of the pocket and gradually assume a bud-like appearance, resembling a pair of imaginal discs (Pl. I. fig. 1 *c*, *pl*). When the larva nears pupation, each bud, by the appearance of an horizontal longitudinal fissure on its mesial face, becomes doubled, so that there are now two pairs of buds (fig. 1 *f*), the rudiments of the lateral lobes (*ll*) and of the median lobe (*r.md*) of the image.

The bottom (the anterior end) of the genital pocket is continued, after a constriction, as a narrow duct (*ejd*) inside the body; this is the future ejaculatory duct. Its opening into the pocket (*o.ejd*) lies between the bases of the rudiments of the median lobe (figs. 1 A & 1 A).

The spiculum (Pl. I. figs. 1 *a* & 1 *c*, *sp*) arises, while the individual is still in the larval stage, as a pair of ectodermal invaginations of the body-wall just posterior to the ninth sternite; the invaginations lie, one on either side of the genital pocket. The fact that the spiculum is present in the larva, in which the ninth sternite is also distinct, establishes beyond any doubt that this organ in the imago is not the modified ninth sternite, as it was believed to be by numerous investigators, *e. g.*, Hopkins (**10**), etc.

During pupation the genital pocket enlarges very much; it becomes wider and deeper, and its bottom evaginates, carrying the rudiments of the lateral lobes and the median lobe towards the posterior, the latter lying at the apex of the evagination. Text-figures 1 and 2 illustrate the organs before and after pupation. This evagination is the future tegmen; its ventral region gradually thickens into a plate-like sclerite. The body segments do not undergo any appreciable change, when the individual pupates; the nine distinct tergites and sternites can still be recognized. The tenth segment is also of the same form as in the larva (Pl. II. fig. 2 A). The genital papillæ in the pupa are rather stiff, resembling a pair of conical appendages bordering the opening of the genital pocket. Their bases are fused with each other and are flush with the ninth sternite (Pl. II. figs. 2 *a* & 2 *b*). Just dorsal to their base the body-wall is invaginated, forming a shallow cavity (*g.c*, text-fig. 2), which persists even in the adult stage (Pl. III. fig. 3 *a*).

Hopkins (10) considered the tegmen to be an apodeme of the ninth tergite; Bugnion (5) imagined it to be a part of the tenth segment; Peytoureau (16) homologized this organ with the ninth sternite. The fact that in the pupa all these parts, as well as the tegmen, are present clearly indicates the untenability of the theories of these authors.

In the pupa, the two rod-like rudiments of the median lobe, which are hollow and are depressed on their mesial faces, each appearing ℂ shaped in a cross section, gradually come near and actually fuse with each other, first only along their dorsal margins, so as to assume the form of a single two-layered organ with a deep ventral groove; the inner layer of the organ is

Text-figures 1 and 2.
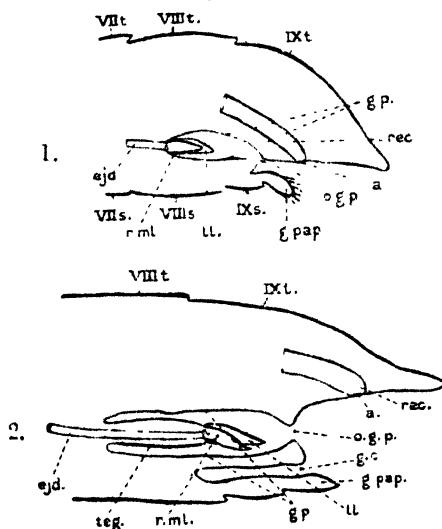
Tenebrio molitor. Longitudinal vertical sections through the posterior region of the abdomen of larva and pupa. (1) Larva; (2) pupa. Diagrammatic. To illustrate the changes during pupation.

proximally continuous with the ejaculatory duct which in the larva was ending between the bases of the median lobe-rudiments. Then by the blending together of the lips of the groove the organ is turned into a double-walled tube, one tube within the other, the inner constituting the distal region of the ejaculatory duct, the outer being the wall of the median lobe itself. The lateral lobes by fusing with each other in their proximal region, above and below the base of the median lobe, surround the latter in a ring-like fashion. Figs. 2 a–2 k (Pl. II.) illustrate the organs of a five-days old pupa as seen in a transverse section in the different regions of the body (from the posterior towards the anterior). It will be observed that the median lobe is still in

the form of a pair of appendages in its extreme distal region
(figs. 2 *d* & 2 *e, r.ml*).

When the pupa transforms into the imago, the genital
papillæ are cast off; the ninth sternite itself is dechitinized and
becomes altogether indistinguishable from the membranous area
between it and the anus, and thus forms a part of the wall of
the genital pocket. The eighth and the following abdominal
segments are withdrawn into the preceding ones. The different
genital organs by simple growth, heavier chitinization, greater
development of the associated muscles, etc. reach the stage
characteristic of the beetle.

Homologies.—The above-described mode of development of the
genital organs, in essentials, is similar, step by step, to what I
described in the Homoptera (**21**).

The genital papillæ, on account of their form and position
obviously represent the coxites of the ninth sternum. However,
they do not persist beyond the pupal stage. The lateral lobes
and the median lobe, developing from an originally single pair
of appendages which are the diverticula of the body-wall between
the ninth and tenth sterna and which subsequently become
two pairs, undoubtedly correspond to the parameres and ædeagus
respectively of other insects.

Unlike the condition in Coleoptera and a few other groups of
insects, in most Orders, *e. g.*, Hymenoptera, Lepidoptera, Diptera,
etc., the coxites are invariably distinct and very conspicuous even
in the imaginal condition. Therefore there is a great temptation
for investigators working on Coleoptera, etc., unless they study
the development, to interpret the lateral lobes as coxites. And
curiously enough Muir (**13**), who had observed that in the larvæ
and pupæ of some beetles, *e.g. Cistela*, there is a pair of
appendages attached to the posterior margin of the ninth
sternite, and that the lateral lobes do not develop as do the
coxites in other insects, has also succumbed (though not readily)
to this temptation. In addition to the direct ontogenetical
evidence, given in the preceding pages, showing that the lateral
lobes of Coleoptera are equivalent to the parameres of other
insects and that the coxites are represented by the genital
papillæ, the reader is referred to my above quoted paper in
which I discussed the question on a purely morphological and
anatomical basis and gave numerous reasons why the lateral
lobes could not be the coxites.

The tegmen is nothing but a diverticulum of the body-wall
at the base of the median lobe and the lateral lobes. No part
of the genitalia is derived from a sternite or a tergite of a body
segment.

(b) *Efferent Genital System.*

In a fully-grown larva (Pl. I. figs. 1 A & 1 A'), as already
described, the bottom of the genital pocket is continued as a
narrow duct (*ejd*) inside the body, the rudiment of the common

ejaculatory duct; the latter at this stage extends up to the posterior region of the eighth segment. The testes and the vasa deferentia can also be easily recognized ; the latter, quite narrow and almost thread-like, extend up to the common ejaculatory duct, where they open into a pair of rounded vesicle-like structures (*ectd*), the future ectadenia. The ectadenia are located one on either side of the short ejaculatory duct, butting against but not opening into it (Pl. I. figs. 1 *b* & 1 *d*).

The ectadenia and the vasa deferentia are similar to each other in all essentials (Pl. I. figs. 1 *b* & 1 *d*) ; both consist of an internal prominent epithelial coat and an external thin muscular coat ; the epithelial cells of the former are, however, somewhat swollen. Moreover, the lumen of the ectadenia is lined by a structureless film-like substance which appears yellow, as does the chitinous lining of the ejaculatory duct, when stained with iron hæmatoxylin. The vasa deferentia have no lumen at this stage. Figure 1 *b*, which is a drawing of the section cutting the vasa deferentia and the ectadenia in a longitudinal plane, clearly

Text-figure 3.
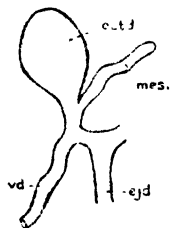
Tenebrio molitor.   Region of junction of the ejaculatory duct, ectadenium, mesadenium, and vas deferens.

shows that the latter are nothing more than the swollen ends of the former.

The epithelial cells of the ejaculatory duct, though slightly different in shape and comparatively smaller, take the same stain as those of the ectadenia and the vasa deferentia. The hypodermis also takes a stain similar to these organs.

During pupation the distal ends of the vasa deferentia, near the base of the ectadenia, open into the ejaculatory duct (text-fig. 3).

The mesadenia (text-fig. 3) make their appearance in the early pupal stage as a pair of anteriorly directed diverticula, one from each vas deferens, from near the bases of the ectadenia.

In the pupa, the ejaculatory duct gradually elongates, its proximal or anterior end extending into the fifth or fourth abdominal segment, and consequently throwing the vasa deferentia into a coil.

Thus there does not appear to be any evidence whatever in favour of the conclusion of Escherich that the ectadenia are of a

different origin from the vasa deferentia ; both are histologically similar, and in fact the former do not appear to be distinct organs at all, but the modified distal ends of the latter. If the drawings of Escherich or of Blatter be carefully examined, it will be noticed that there is not so much difference between the two organs as they claim in the text.

So the ectadenia and the vasa deferentia are parts of the same organs, but the further question, whether they are mesodermal or ectodermal structures, cannot be answered with certainty without following their embryological history. Bordas believed that they are mesodermal, but as appears from their histological structure, which exactly resembles that of the ejaculatory duct, an hypodermal invagination, it seems that they, both of them—and not ectadenia alone as believed by Escherich —are ectodermal in origin. No doubt these organs, especially in the imago, are devoid of a chitinous lining, but, as was also pointed out by Escherich, this seems to be due to the fact that they take up another secretory function, viz., that of producing the substance used for the formation of spermatophores, etc. Moreover, all ectodermal epithelia do not necessarily have a chitinous intima, e. g., the malpighian tubules, admitted on all hands to be diverticula of the proctodeum, are without such a lining.

To interpret the vasa deferentia as ectodermal structures looks like a paradox, and it seems that it is chiefly due to this that most of the previous investigators refrained from interpreting them so. But it appears that the organs so called in Coleoptera are not homologous to the vasa deferentia of other insects. Wherever the development of the genital organs has been studied it is found that the vasa deferentia do not extend beyond the seventh abdominal segment, while the so-called vasa deferentia of Coleoptera, as mentioned above or described by Muir, are found extending up to the posterior margin of the eighth sternite. Moreover, the vasa deferentia are believed to be nothing but mere prolongations in the posterior direction of the epithelium covering the testes; but the examination of figure 3 e (Pl. III.) will show that this is not the case in Coleoptera, the epithelial covering of the testes being quite different from the epithelial lining of the vasa deferentia.

In this connection an isolated remark of Muir, unsubstantiated by any histological evidence, is of great interest : " The zygos (vasa deferentia) are supposed to be of mesodermic origin, but they seem to develop continuously from the stenozygos (ejaculatory duct)," viz., Muir implied that the vasa deferentia are ectodermal structures, a statement in full accord with what I have established in the above paragraph.

A question will naturally be asked : where are the true mesodermal vasa deferentia in Coleoptera? It appears that they, especially in the imaginal stage, do not extend beyond the region of the testes. That this is so is supported by the fact

that Saling (18), who studied the embryology of the genital
organs of *Tenebrio molitor*, fortunately the same form whose
post-embryonic history is being detailed in the present paper,
describes the mesodermal vasa deferentia to be extremely short
and not extending up to the base of the ninth segment as do the
so-called vasa deferentia.

In Homoptera I (21) described a pair of ectodermal ducts origi-
nating from near the posterior margin of the eighth sternite,
which, as development proceeds, at their anterior ends get into
communication with the vasa deferentia, and posteriorly open
into the common ejaculatory duct. These ducts, which were
designated as the paired ejaculatory ducts, were compared with
the ectodermal " paired anlage" in the efferent genital system
described by Nussbaum in Mallophaga, Culicidæ, Blattidæ,
etc. If the development of the vasa deferentia as given in the
preceding pages be recalled, an exact similarity between them
(along with the ectadenia) and the paired ejaculatory ducts of
Homoptera will be noticed. Moreover, as accessory glands
arise from the paired ejaculatory duct, so do the mesadenia
from the vasa deferentia in Coleoptera. The only difference
between the efferent systems of the two groups is that the true
vasa deferentia in the Coleoptera are considerably reduced if not
totally obliterated.

As a natural consequence of his interpretations Escherich com-
pared the ectadenia alone with the paired " ectodermal anlage"
of Nussbaum. Leaving other things aside, a very strong
objection to this is that while the latter get connected with the
vasa deferentia at their distal ends, the ectadenia according to
Escherich's conclusions do so at their proximal ends; and their
distal apices end blindly in the body-cavity. Escherich was not
unaware of these objections, but he could not explain them.
According to my interpretations there is no occasion for
questions of this kind.

In view of the fact that the vasa deferentia of Coleoptera are
not the true vasa deferentia, to avoid confusion they must be
designated differently. In the absence of a better term they
may be called " paired ejaculatory ducts," an appellation which
was given to the organs of Homoptera of which, as above shown,
they seem to be homologues.

According to Wheeler (23) in *Xiphidium* (Orthoptera) there
is no organ corresponding to the above mentioned paired " ecto-
dermal anlage" of Nussbaum. Wheeler even went so far as
to doubt the existence of such organs in the Insecta altogether.
But Nussbaum's view, at least on this point, is receiving fresh
support day after day. It appears that in Orthoptera the
condition of the efferent system is similar to what it is in
Coleoptera. The vasa deferentia and the terminal ampullæ
as described by Wheeler seem to be similar to the vasa
deferentia and ectadenia described in the previous pages. But
Wheeler explicity declared these organs to be mesodermal in

origin. That they may not be so is suggested by the fact that while he describes the vasa deferentia as extending up to the region of the ninth segment (an unusual feature), he mentions the oviducts as ending near the posterior margins of the seventh only. It is highly probable that the vasa deferentia also do not extend so much and that their posterior parts are of a different origin. That it may be so is suggested by the observations of Heymons (9) on the Blattid genus *Phyllodromia*, in which he described the distal regions of the vasa deferentia to be forming anew. But Heymons did not go into this question in detail and did not say whether the newly formed parts were mesodermal or ectodermal. In any case Wheeler's observations require confirmation.

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EXPLANATION OF PLATES I., II., III

LETTERING.

a	= anus.	*o g p*	= opening genital pocket.
bc	= body cavity.	*pl*	= paramere lobes.
b.g pap	= base of the genital papillæ.	*r.ml*	= rudiments of the median lobe
ct	= chitinous cuticle.	*rec*	= rectum.
ect	= ectoderm.	*sm*	= intersegmental membrane.
ectd	= ectadenia.	*sp*	= spiculum.
ejd	= ejaculatory duct.	*st*	= struts of the median lobe.
ejd¹	= bifurcations at the anterior end	*teg*	= tegmen.
	of the ejaculatory duct.	*tes*	= testes.
gnp	= gonopore.	*tr*	= tracheæ.
g.p	= genital pocket.	*vd*	= vasa deferentia.
g pap	= genital papillæ.	I--X	= the different abdominal seg-
hyp	= hypodermis.		ments.
ll	= lateral lobes.	I_t--X_t	= tergites of the different abdo-
mesd	= mesadenia.		minal segments.
ml	= median lobe.	I_s—X_s	= sternites of the different abdo-
n.c	= nerve cord.		minal segments.

PLATE I. LARVA.

Fig. 1 A. Ninth and tenth abdominal segments and the genital organs. Ventral view. × 40. The genital pocket has been cut open.

Fig. 1 A'. The genital pocket with its contents enlarged.

Figs. 1 a-1 f. Transverse sections through the different regions of the tip of the abdomen.

  1 a 1 b. Middle-aged larva; from posterior towards the anterior. × 65.

  1 c 1 d. Fully-grown larva; from posterior towards the anterior. × 80.

  1 e-1 f. Larva ready to pupate; from posterior towards the anterior. × 120.

PLATE II. PUPA.

Fig. 2 A. Posterior abdominal segments, ventral view. × 15. The genital pocket cut open.

Figs. 2 a-2 k. Transverse sections through the different regions of the posterior abdominal segments—from posterior towards the anterior.

  2 a-2 d. × 50.   2 e-2 g. × 65.   2 h-2 k. × 120.

PLATE III. IMAGO.

Fig. 3 A. Dissection of the genital organs.

3 B. Posterior abdominal segments and the external genital organs. Dorsal view. (After treatment with KOH.)

3 C. Transverse sections—Ectadenium, Mesadenium, Vasa deferens, and Ejaculatory duct. Equally magnified. *sec* = secretion.

Figs. 3 *a*-3 *e*. Transverse sections through the different regions of the abdomen—from posterior towards the anterior. × 50.

3 *a*. Through the region where the proximal region of the lateral lobes surrounds the base of the median lobe in a ring-like fashion.

3 *b*. Slightly anterior to the above.

3 *c*. Through the tegmen.

3 *d*. Where the tegmen becomes continuous with the wall of the genital pocket.

3 *e*. Through the region of the testes.

FEMALE GENITALIA OF TENEBRIO MOLITER.
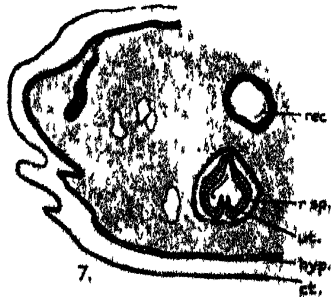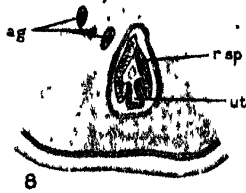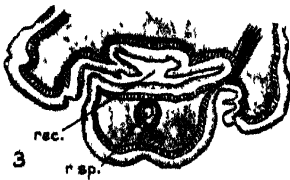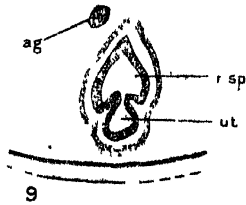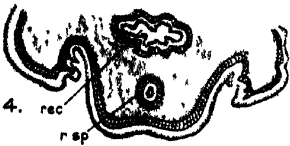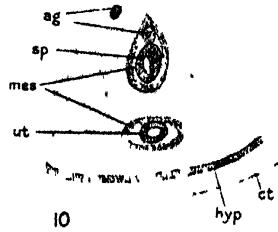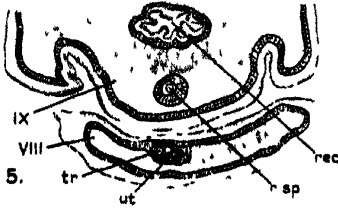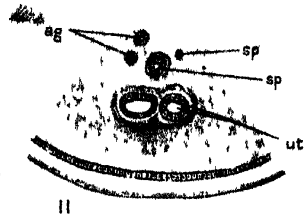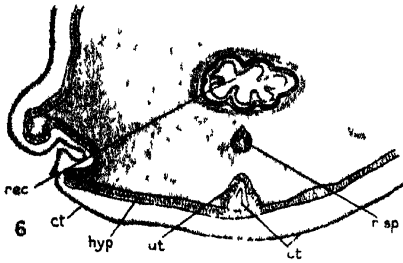
38. On the Development of the Ovipositor and the Efferent Genital Ducts of *Tenebrio molitor* L. (Coleoptera), with Remarks on the Comparison of the latter Organs in the two Sexes. By HEM SINGH PRUTHI, M.Sc. (Punjab) *. (From the Zoological Laboratory, Cambridge.)

(Plate IV.† ; Text-figures 4–10.)

a. OVIPOSITOR.

There exists a great deal of difference of opinion with regard to the nature of the ovipositor in Coleoptera. The three pairs of ovipositor-lobes, present in a typical insect, are supposed to be totally unrepresented in this Order. The gonopore is bordered by a pair of plates which bear palpiform appendages at their apices (text-figs. 6 & 7, *gp*) : no two investigators have interpreted these plates in similar terms. They were labelled as the divided ninth sternite by Stein ('47), as the tenth sternum by Verhoeff ('93), as the eleventh by Berlese ('09), while Peytoureau ('95) designated them as the eighth sternum in some families and as the seventh in others. The belief that the ovipositor in this Order is not a true ovipositor, viz., it is not comparable to that of groups like Hymenoptera, Homoptera, etc., but is constituted by a posterior body-segment, is not restricted to the above named authors but is quite general (Korschelt & Heider, etc.). It seems that this hypothesis has never been vindicated by an examination of the organs in the larva or pupa. From my ontogenetical studies on *Tenebrio molitor*, carried on during the last few months, it appears that the plates under review do not represent a sternite, etc. of any body segment but correspond to one of the three usual ovipositor-lobes ; therefore no apology is needed for communicating the results of these studies.

In the larva (text-figs. 4 & 8) nine distinct terga and sterna can be easily recognized. The ninth segment is somewhat different in form from the preceding ones. Its tergal region, as compared with the sternal, is very much enlarged, and is bent down in the posterior region, with the consequence that the anus (*a*) lies on the ventral side of the body instead of at its posterior end. The anal opening is borne by a membranous

* Communicated by F. BALFOUR BROWNE, M.A., F.Z.S.
† For explanation of the Plate see p. 883. The lettering of the text-figures and plate-figures is uniform.

papilla (X) which might represent the dechitinized small tenth segment. The body-wall between this papilla and the narrow ninth sternite (*sm*) is membranous and bears, just behind the latter, a pair of small, blunt, hollow and hairy appendages (*gp*), one on either side of the median line ; between the bases of these appendages there is a small opening (*gnp*), the future gonopore. The appendages, therefore, will be referred to as the genital appendages in the following descriptions.

In the pupa (text-figs. 5 & 9) the body-segments are almost of the same general form and appearence as in the larva. The genital appendages are, however, slightly different; they are stiff, conical, devoid of hairs, and have pimple-like appendages (*st*) at their apices. Their bases are hardly distinct from the

Text-figure 4.
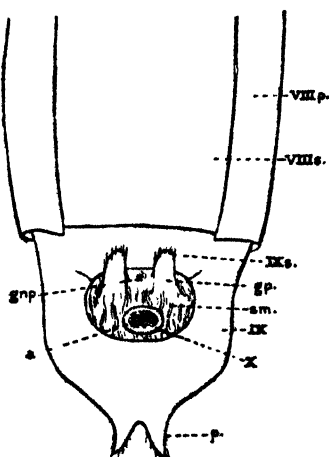
Ventral view of the posterior abdominal segments of the larva.

ninth sternite. The gonopore is still at the same place, and figures 1–3 (Pl. IV.), illustrating the sections of body in this region (from the posterior towards the anterior), show how the mesial faces of the genital appendages are continuous with the wall of the vaginal canal (*r.sp*).

When the pupa transforms into the imago, the body-segments undergo considerable modifications. But, if the text-figure 6 of the abdomen of the beetle be compared with text-figures 8 & 9 of the same region of the larva and pupa, the change of shape and size undergone by this part of the body in the passage from the larval to the imaginal state can be easily appreciated, and the different segments at once recognized. The sixth is the last visible segment; the major portion of the seventh and the following segments are retracted into it. Moreover, the eighth, on

account of the fact that its posterior region has been dechi-
tinized, appears shorter than it is in the pupa or the larva.
Similarly the anterior region of the ninth has been membranized;
thus the intersegmental area between the two segments has been
considerably enlarged ; this provides for the ninth being tele-
scoped into the eighth. The ninth sternite (IX$_s$) itself is
membranous and hardly recognizable as a distinct sclerite.
Moreover, the tergal region of this segment is no longer bent
down in its posterior region, so that the anus is now at the
distal extremity of the body. For the same reason, the genital
appendages, though virtually in the same position, are also no
longer on the ventral side, but at the apex of the body, below
the anal opening. They are slightly more elongated, and are
fused with each other for most of their length. The pimples at
their apices are more or less palpiform. The gonopore is at the
same place, but in consequence of the above mentioned fusion of

Text-figure 5.
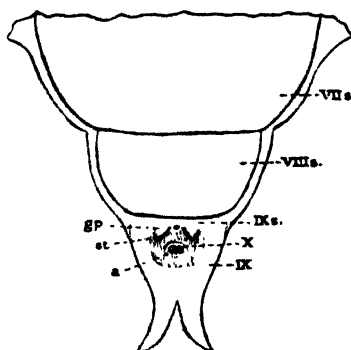
Ventral view of the posterior abdominal segments of the pupa.

the appendage to a greater extent, it has shifted caudad ; it now
lies between the apices of the appendages instead of between
their bases.

Evidently the genital appendages or plates of the imago
which have been traced to a pair of appendages, distinct
from a sternite or other part of any body-segment, in the larva
and pupa, do not represent any such part, as has been hitherto
believed. That the appendages under discussion of the larva
are really the rudiments of the genital appendages of the adult
was verified by an amputation experiment also : one of the
appendages of the larva was cut off, and in the pupa and the
beetle the corresponding plate was found missing.

Appendages corresponding to the genital appendages of *Tenebrio*
can be recognized in the larvæ and pupæ, especially the latter, of
most Coleoptera.

The genital appendages, as was also shown in the case of the

male (Singh Pruthi, '24²) *, where, however, they do not persist
beyond the pupal stage, on account of their form and position,
behind the ninth sternite, seem to represent the coxites of this
segment.   The palpi at their apices therefore may correspond to
the styli.

It is now almost unanimously accepted (see Singh Pruthi, '24¹)
that the three pairs of ovipositor-lobes, the anterior, the dorsal
and the posterior, represent the endopodites of the eighth, and the
endopodites and coxites of the ninth segment respectively.   The
genital appendages of Coleoptera, being the coxites of the ninth
segment, therefore correspond to the posterior pair of ovipositor-
lobes.   The only modification that they have undergone is that
they are more or less fused with each other almost throughout
their length.   But such a fusion of the ovipositor-lobes is not
uncommon in the Insecta.   In Hymenoptera, Rhynchota, etc.,
the dorsal lobes are fused with each other throughout their

Text-figure 6.
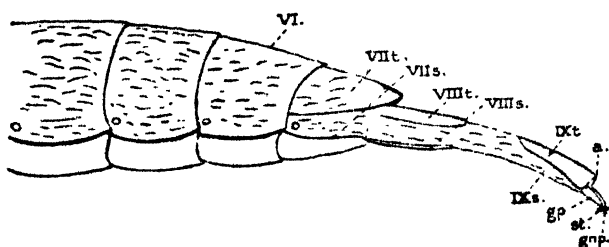
Lateral view of the abdomen of the imago (Potash preparation).
Terminal segments pulled out.

length, though only along one border.   Moreover, in all Coleoptera
the genital plates do not show the above modification ; in forms
like *Dytiscus* and *Hydrophilus* they are quite distinct from each
other (Berlese, '09, figs. 341 & 337).

In Diptera, Lepidoptera, etc. also the ovipositor is con-
sidered to be constructed out of posterior abdominal segments and
not to be comparable to a true ovipositor (Kolbe, '93, etc.).   It is
highly probable that the condition in these Orders is similar to
that in Coleoptera, because in the younger stages of these groups
there is a pair of appendages, which in the case of the male
develop into the "claspers," "valves," etc, and the latter are
generally accepted as being the coxites of the ninth segment
(Christophers, '22, Muir, '23, etc.).   In the case of the female,
however, the fate of these appendages has not yet been traced,
but as follows from their condition in the male, it is highly
probable that they are coxites in this sex also.   The organs

* The appendages in that sex were termed " genital papillæ."

labelled " ventral Klappen " by Stitz ('01) in some Lepidoptera and those marked "anal scales" by Lowne ('95-98) in the Blow-fly (his fig. 107 A, p. 746) certainly remind one of the genital appendages of *Tenebrio*. Kulagin ('01) also described a pair of appendages near the genital opening in some Diptera. More-over, as appears from the drawings of Poulton ('88) and Jackson ('88), the structure of the terminal abdominal region of Lepi-doptera is, in essentials, similar to that in Coleoptera, the organs designated as " eminences representing the prolegs" corresponding to the genital appendages of *Tenebrio*, but these authors interpret as the tenth segment what has been labelled as the ninth by me in Coleoptera.

In the above paragraph I referred to the work of Stitz ; and I may remark in this connection that Stitz in his figures 137-150, illustrating the transverse sections of the abdomen, seems to have labelled the parts not quite correctly, *e. g.*, the organ marked " vagina " appears to be rectum and vice versa. A comparison of his drawings and mine illustrating these organs (Pl. IV. figs. 3-6) will clearly show what I mean.

b. INTERNAL DUCTS.

The morphology of the efferent genital system, uterus, sperma-theca, etc., in Coleoptera, or in any other Insect Order, is still not clear. In Ephemeroptera there is a pair of genital openings located behind the seventh sternum (Palmén, '84) ; in most insects there is a single opening and it lies between the eighth and ninth sterna ; in Lepidoptera there are two openings, not on the same segment, however, but one at the posterior margin of the eighth sternite, the other at the same position on the ninth (Jackson) ; in Diptera (Berlese, '09) and, as shown in the preceding pages, in Coleoptera there is a single vaginal aperture which is located behind the ninth segment. Is the genital opening in the different groups the same morphologically, viz., is its variability in position simply due to a forward or backward displacement ? This question has not yet been answered ; moreover, the answer is likely to settle the true comparison of the internal ducts in the two sexes. The usual comparison, found in almost all the text-books, the homologizing of the uterus with the common ejaculatory duct, is open to a serious objection. The latter, as is well known, originates in all insects from behind the ninth sternite and is unpaired from the very beginning (Korschelt & Heider, Wheeler, '93, Singh Pruthi, '24[1] & '24[2]), while the uterus or the azygos oviduct, as above mentioned, opens in most insects between the eighth and ninth sterna, and is paired in origin in many Orders (Herold, '15, Suckow, '18, Verson & Bisson, '96, Nüssbaum, '84). The developmental history of the genital ducts of a member of the Coleoptera, in which group the vagina, unlike that in most other insects, opens behind the ninth segment,

is sure to throw some light on the above questions, and is described in the following pages.

The general form and arrangement of the reproductive organs of the female is well known (see Stein), so the following brief description and the text-figure 7 are given simply to furnish a standard of reference for the developmental history.

The two ovaries (*ov*) extend up to the posterior region of the fifth or sixth abdominal segment. The oviducts (*ovd*) are short; about the posterior region of the seventh segment they open into the common oviduct. The latter, which will be

Text-figure 7.
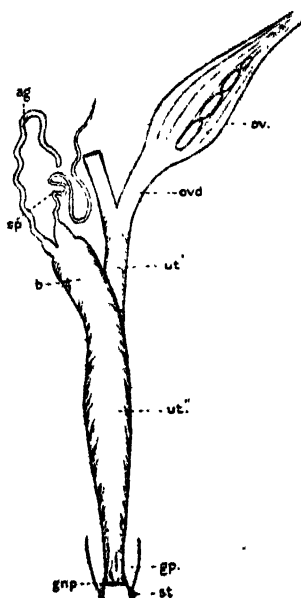
Surface view of the reproductive organs of the imago.

designated as uterus, is very long, opening behind the ninth segment, and is differentiated into two distinct regions, the short and narrow proximal (*ut'*) and the long and wider distal (*ut''*), the Eiergang and Scheide respectively of Stein. The distal part of the uterus is proximally produced into a laterally directed bag-like pouch (*b*), in which the tubular spermatheca (*sp*) and the accessory gland (*ag*) open.

In a fully developed larva (text-fig. 8), an invagination of the body-wall behind the ninth sternite (*r.sp*) extends anteriorly up to the eighth abdominal segment. This is the rudiment of the spermatheca; its opening (*gnp*) is the future gonopore.

In a young pupa (text-fig. 9 & Pl. IV. figs. 1–6) the sperma-
thecal invagination is in the form of a distinct tube, especially in
its posterior region, and it extends much more anteriorly. More-
over, at this stage another tube (*ut*), not quite duct-like, can be
made out in the posterior region of the abdomen, beginning from
near the posterior margin of the eighth sternite. This is the
rudiment of the uterus. It resembles the spermathecal invagi-
nation and the general hypodermis in its structure, therefore
there is no doubt that it is ectodermal in origin. The uterus
rudiment, very narrow in the posterior region, gradually widens
anteriorly (Pl. IV. figs. 5 & 6). It lies under the spermathecal
invagination.

The uterus in many other insects is described as making its
appearance as a pair of vesicles in the larva, which coalesce with
each other, forming a single organ, in the quiescent period pre-
ceding pupation (Herold, Nüssbaum, etc.). In order to see if this

Text-figure 8.
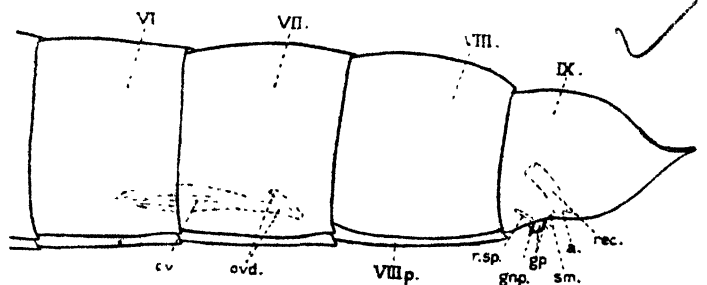
Lateral view of the abdomen of a fully-grown larva—diagrammatic ;
reconstructed from serial transverse sections.

is also the case in *Tenebrio molitor*, numerous old larvæ were
sectioned, but I was not able to find any such paired rudiments
of the uterus.

As the pupa grows older (text-fig. 10), both the spermatheca
and the uterus rudiments become much wider, and the former in
its posterior region comes to rest on the latter with the result that
its ventral wall is pushed up, thus giving rise to a groove in
which the uterus lodges (Pl. IV. figs. 7–11). Gradually the walls
intervening between the two organs (the mid-ventral region of the
spermatheca and mid-dorsal of the uterus) disappear so that their
cavities freely communicate with each other. Pl. IV. figs. 7–10
of the drawings of the sections through the region of commu-
nication of the two organs explain clearly the above-stated
changes.

The uterus does not open out at its normal place, the posterior
margin of the eighth sternite. It, so to speak, opens into the
spermathecal rudiment and communicates with the exterior
through the opening of the latter, behind the ninth sternite.

Anteriorly (Pl. IV. figs. 10 & 11), the uterus bifurcates; the spermathecal rudiment also by a constriction in the longitudinal horizontal plane becomes doubled, giving rise to a narrow dorsal and a wider ventral tube, the rudiment of the accessory gland (*ag*) and the spermatheca proper (*sp*) respectively (text-figs. 9 & 10).

By the time that the imago emerges, the region of communication of the spermathecal rudiment and uterus (*ut''*, text-fig. 7) has grown very much both in its length and width, and is, in fact, the most conspicuous part of the efferent system. This is the distal of the two parts into which the uterus is differentiated. Evidently, therefore, only the short anterior part of the uterus of the imago (*ut'*, text-fig. 7) is derived from the pupal uterus, its larger posterior portion (*ut''*) being developed partly from the pupal uterus (ventral half) and partly from the spermathecal rudiment (dorsal half). From the above it also

Text-figure 9.
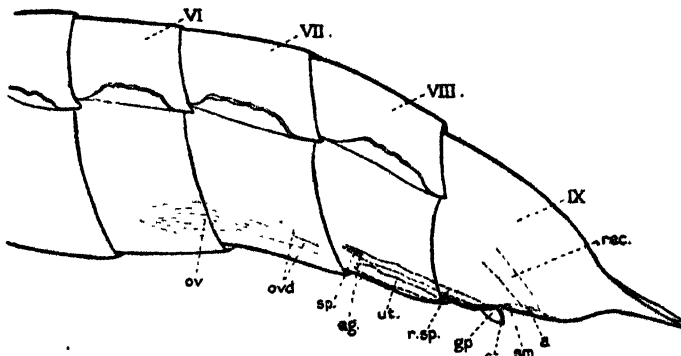
Lateral view of the abdomen of a young pupa—diagrammatic; reconstructed from serial transverse sections.

follows that the part usually described as the diverticulum of the uterus (Stein, etc.), labelled (*b*) in my text-figs. 7 & 10, is really not a part of the uterus at all, but is part of the spermathecal rudiment.

As a natural consequence of the above changes the accessory gland and spermatheca proper lie much anteriorly, and moreover they, in the imaginal state, do not lie one over the other or both above the uterus, but are inclined to the side (left), the accessory gland, which was the most dorsal organ in the pupa, lying farthest from the median line.

Meanwhile communication has also been established between the anterior bifurcated end of the uterus and the distal ends of the mesodermal oviducts.

The connective tissue and the muscles of the above organs arise from the mesenchyma-like tissue present in the body-cavity.

The above brief account leads one to the following conclusions :—

That of the efferent genital system, all the organs (uterus, spermatheca, accessory glands, etc.), excepting the paired oviducts, are of an ectodermal origin. This is exactly what Nüssbaum found in the case of Blattidæ, Culicidæ, Mallophaga, etc. But there is no evidence in support of the further conclusions of this author that the spermatheca and accessory glands, unpaired organs in the imago, arise from paired rudiments. They, as shown in the preceding pages, are unpaired from the very beginning, rather both of them originate from a single hypodermal invagination. In this connection I may mention that in the case of the male also, while I could ('24²) confirm his conclusion that all organs posterior to the vasa deferentia are ectodermal, I could

Text-figure 10.
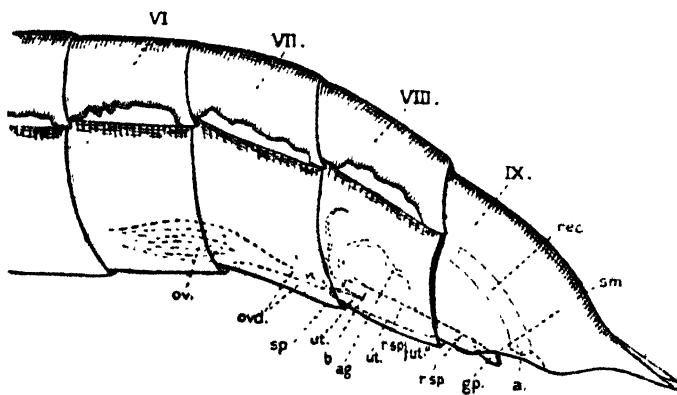
Lateral view of the abdomen of an old pupa—diagrammatic ;
reconstructed from serial transverse sections.

not do so with regard to the origin of the common ejaculatory duct, which I showed to be developing from an unpaired rudiment, while he had concluded that it is paired in origin.

Wheeler ('93) differed from Nüssbaum in all particulars, both with regard to the male and the female. He believed that in both sexes, excepting the extreme terminal section, the whole efferent system is derived from mesoderm. With regard to the male I refuted almost all of his arguments in my papers referred to above. In the case of the female his own figures and descriptions commit him, and Verson & Bisson also, who supported him as regards the structures in the male, differ from him in the case of the female. In this sex Wheeler described the embryonic mesodermal oviducts swelling at the distal ends, forming terminal ampullæ, and ending about the posterior margin

of the seventh sternum. He described and figured another pair of ampulla-like structures located in the posterior region of the abdomen (according to him in the tenth segment), whose presence he could not explain. According to him these ampullæ disappear very soon and correspond to the terminal ampullæ of the male. Obviously Wheeler knew that this interpretation was illogical and open to a serious objection, as he himself remarked that the presence of two pairs of terminal ampullæ in the female was rather a "curious fact." Now, if his description of the second pair of ampullæ be carefully studied, a close similarity between them and the ectodermal paired uterus-rudiments described by Herold, Verson & Bisson in the young Lepidoptera will at once be noticed. Therefore it is highly probable that these "ampullæ" in *Xiphidium* give rise to the uterus as the ectodermal paired rudiments are described to do in Lepidoptera, etc. If this is so, then the ampullæ under review should be ectodermal structures and should lie near the posterior margin of the eighth segment, and not in the tenth as Wheeler describes. As regards the demarcation of the body-segments, Wheeler was not very particular : for example, he located the posterior pair of ovipositor-lobes on the tenth, while everybody else locates them on the ninth ; then, he described the vaginal aperture as being at the posterior margin of the seventh, while it is described in almost all other Orthoptera as at the posterior margin of the eighth (Berlese, '82, Heymons, Haase, '89[2], Walker). To locate the vaginal aperture behind the seventh seems illogical, because this opening is always between the anterior and dorsal pair of ovipositor-lobes wherever the latter are developed, and in the case of *Xiphidium* Wheeler does describe a complete ovipositor. But, as he did not believe that there was any ectodermal section of the efferent system and as the oviducts themselves do not extend beyond the seventh, he had no course open but to locate the vaginal aperture at the posterior margin of the seventh.

The other important conclusion that follows from the account given in the foregoing pages is that the spermathecal rudiment originates independently of the uterus and it is at a later stage that the two open into each other. This, while in accord with the observations of Herold and Berlese, is in contrast with the conclusions formulated by Jackson, Balbiani ('72), Weismann ('64), Witlaczil ('84), Anton Schneider ('83), etc., that the accessory female organs are outgrowths of the vagina or uterus itself. These investigators probably overlooked the condition in the earlier stages, as their statements are quite true of the older pupæ, when the cavity of the spermathecal rudiment is communicating with that of the uterus and the former appears to be a diverticulum of the latter.

To discuss the position of the genital aperture I shall have to recapitulate the main facts of development. The paired

oviducts (mesodermal) end in the posterior region of the seventh
segment.   The common oviduct or the uterus (ectodermal)
originates from near the posterior margin of the eighth sternum.
The rudiment from which the spermatheca and the accessory
gland develop is an invagination of the integument from behind
the ninth sternite.   The spermatheca and the uterus secondarily
open into each other.

In Ephemeroptera, etc., where there is a pair of genital
apertures, lying behind the seventh sternite, it seems that the
latter represent the opening of the mesodermal paired oviducts
and that there is no part corresponding to the above described
uterus, etc.; *i.e.* the ectodermal portion of the efferent system
is totally undeveloped in these groups.   This is in strict
accordance with the anatomical observations of Palmén ('84).

In most insects, where there is a single vaginal aperture
which lies between the eighth and ninth sterna, it appears that
the opening in question is the opening of the uterus proper and
that the opening of the spermatheca (behind the ninth sternite)
has been obliterated, the organ communicating with the
exterior through the opening of the uterus. This hypothesis
is supported by the facts observed by several investigators.
e. g., Berlese ('82) in Mantidæ, 'Locustidæ,' Gryllidæ, etc.   (See
Berlese ('09), fig. 1130 *d*, p. 867.)

In Coleoptera, where the single genital aperture lies behind the
ninth segment, it has been shown in the preceding pages that
it is really the opening of the spermatheca, and that the uterus
in this group does not open out but opens into the spermatheca
and thus communicates with the exterior by the opening of this
organ.   In Diptera also, where there is only one opening and
that behind the ninth segment, it appears that the condition is
similar to that in Coleoptera.

In Blattidæ, Acridiidæ, and most Lepidoptera, there are two
genital apertures, one on the eighth and the other on the
ninth.   Nüssbaum in the case of Blattidæ and Berlese in that
of Acridiidæ showed that the anterior opening is that of
the uterus and the posterior that of the spermatheca.   This
is what I would also say in light of the above stated facts.
In Lepidoptera also one would interpret the openings in
similar terms.   But Jackson in his well-known studies ('88)
explicitly designated the openings in the reverse order.   This
naturally involved him in many complications: Why and how
does the uterus opening migrate from the eighth (its normal
position in the Insecta) to the ninth?   How do its different
parts originate? etc.   The major portion of his paper is devoted
to attempting to explain these points, which he fails to do, as
at the end of his paper he gives some of the above questions and
remarks that further investigations are necessary.   Not only the
above but many more objections must be answered before his

interpretations can be accepted : Why should the spermathecal opening, primitively behind the ninth sternite in all other insects, be behind the eighth in Lepidoptera ? Secondly, why should the spermatheca, an organ unpaired in origin in most Insecta, be paired in this Order ? Thirdly, this organ, while it opens into the uterus at a later stage of development in other insects, and even in Lepidoptera (Herold), is, according to Jackson's interpretations, in communication with this organ from the very beginning.

But the drawings and descriptions of Jackson, which seem to be quite accurate, show that the condition in Lepidoptera is as expected, and not as Jackson interprets. According to his descriptions (p. 168) the greater part of the uterus originates as a deep furrow. Now, if the development of the uterus of *Tenebrio* be recalled, it, when a communication is being established between its cavity and that of the spermatheca, appears furrow-shaped (see Pl. IV. figs. 7-11), etc.

Moreover, the descriptions of development of the efferent system given by Herold and Suckow in the case of other Lepidoptera, which have been declared "erroneous" by Jackson, are similar, in the necessary essentials, to what I have given for Coleoptera and what several other investigators have done for other Orders. Moreover, it is interesting to note that Jackson did examine the forms studied by these authors, and remarked that they have got the same rudiments as the forms examined by him. Therefore one feels all the more sure that the forms which Jackson examined are not different from other members of the Order, but that only his interpretation is at fault. If his mind had been free of the notion of the reversal of the position of the two apertures, his story of the development of the organs would have been as simple as can be.

Thus we reach the important conclusion that the genital aperture or apertures in the several groups of insects are not homologous. In some they are the openings of the paired mesodermal oviducts and then they lie behind the seventh ; in others the genital aperture is single and is the opening of the uterus, lying behind the eighth, or it is the opening of the spermatheca when it is located behind the ninth.

As regards the comparison of the efferent systems in the two sexes, it is only with regard to the ectodermal portions that opinions differ, otherwise it is admitted by all that the oviducts correspond to the vasa deferentia. In the case of the male, as I showed in my previously mentioned papers, there is an hypodermal invagination of the body-wall behind the ninth sternite, the rudiment of the common ejaculatory duct. The latter at its anterior end, about the posterior region of the eighth segment, meets and opens into a pair of ectodermal ducts, the paired ejaculatory ducts, which at a later stage of development get into

communication with the vasa deferentia. In the case of the female also, as has been described in the foregoing pages, there is an invagination of the integument from behind the ninth sternite, the spermathecal rudiment, which meets and opens into an ectodermal duct, the uterus, described as arising in many insects by coalescence of a pair of ducts; the uterus at a late stage in development becomes continuous with the oviducts, as do the paired ejaculatory ducts with the vasa deferentia. Evidently, therefore, the common ejaculatory duct of the male corresponds to the spermathecal invagination of the female and not to the uterus, as hitherto generally believed. The homologues of the uterus are the paired ejaculatory ducts. No doubt the latter, in Homoptera and Coleoptera, unlike the uterus, remain paired throughout (Singh Pruthi), but in many other groups they, like the latter, coalesce into a single duct (Nüssbaum).

My sincere thanks are due to Mr. F. Balfour Browne, M.A., for the valuable suggestions that he made with regard to this work.

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EXPLANATION OF PLATE IV.

LETTERING.

a	= anus.	*r.sp*	= the spermathecal invagination which develops into the spermatheca proper and the accessory gland.
ag	= accessory gland.		
ct	= chitin.		
gnp	= gonopore.	*sm*	= intersegmental membrane IX—X.
gp	= genital appendages or plates.		
hyp	= hypodermis.	*sp*	= spermatheca.
mcs	= mesenchyma-like tissue concentrating round the ducts.	*st*	= stylets.
		tr	= trachea.
p	= processes of the ninth segment.	*ut*	= uterus.
ov	= ovary.	I—X	= the different abdominal segments: *t, p* or *s* affixed to these denote the tergum, pleuron or the sternum of the respective segments.
ovd	= oviducts.		
rec	= rectum.		

Figs. 1–6. Serial transverse sections through the posterior region of the abdomen of a young pupa, from the posterior towards the anterior. Section 5 passes through that part where the anterior region of the ninth segment is slightly telescoped into the eighth; the section cuts both the ninth and a part (ventral) of the eighth.

1, 2, 5 × 65.   3, 4, 6 × 50.

Figs. 7–11. Serial transverse sections through the posterior region of the abdomen of an older pupa.

39. The Elasmosaurid Shoulder-girdle and Fore-limb.   By
D. M. S. WATSON, M.Sc., F.R.S., Jodrell Professor
of Zoology, University College, University of London.

(Text-figures 1-12.)

Although the literature of the reptilian order Plesiosauria is
very extensive and the structure of the skeleton in many genera
is as perfectly known as in any living animal, no published
attempts have been made to deduce the musculature and by a
careful study of the possible motions at the articulations to
determine what mode of life was pursued by any member of the
group.

It is my intention to begin in this essay a study of the adap-
tations shown in the Plesiosaur skeleton, taking as one of the
simplest and most striking regions the shoulder skeleton and
musculature.   The group of Plesiosaurs is a most suitable one
for discussion with students as an illustration of the extent and
the limits to which definite direct adaptation to a single simple
environment can be carried ; for the plesiosaur skeleton presents
innumerable adaptive features in all its parts, and the conditions
of life of a marine animal are more readily understood from simple
mechanical considerations than those of an inhabitant of the dry
land, and are indeed often capable of mathematical treatment.

Palæontology differs from Zoology and Comparative Anatomy
in that it has as its study animals not merely of one time, but
of successive ages ; which, even if they are not directly
descended from one another, are still of different generations and
give us, although not the actual "origin of species," the oppor-
tunity of studying the development of structure, which is at
present a much more vital problem.

The true palæontological method as it was introduced by
W. Kowalevski, is to take a series of animals of different
generations which can, by persistent characters, be shown to
form an approximate phyletic series, and study first some one
definite region of the skeleton, relating the changes which are
seen to take place in it to the animal's habits and to any changes
which can be inferred to have occurred in its environment.
The Plesiosaurs, occurring as they do abundantly in marine
rocks of all periods from the Rhætic to the Upper Cretaceous,
and as pelagic animals having a world-wide distribution*, give us
an unusual opportunity of finding such phyletic series.

* *Elasmosaurus* occurs in Kansas, Russia, England, Queensland and New Zealand.

Text-figure 1a.
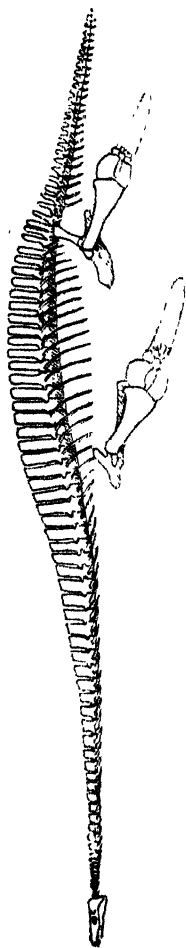
Restoration of the skeleton of *Microcleidus homalospondylus* Owen, from the type specimen.

Text-figure 1b.
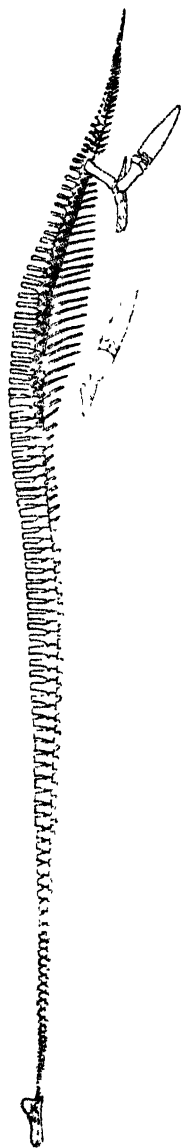
Restoration of the skeleton of *Elasmosaurus*, founded mainly on the type specimen of *E. platyurus* Cope, completed from other material.

No Triassic ancestors of the Liassic Plesiosaurs are known, but it is legitimate to use the Nothosaurs as affording an illustration of the type of shoulder-girdle and fore-limb which must have occurred in them.

A prolonged study of the greater part of the Plesiosaur material in existence in the museums of Britain, France, Germany, South Africa, Australia, and America, shows that the only persistent characters in the skeleton which are available for the discrimination of phyletic lines analogous to those which Prof. Osborn has shown to exist amongst the Perissodactyls, are to be found in the vertebral column, especially in the cervical vertebræ, and in the general proportions.

Amongst the small-headed long-necked Plesiosaurs one series, found in rocks of all ages, is characterized by having middle and posterior cervicals of considerable length, the centra being somewhat wider than high, with a nearly flat ventral surface and lateral surfaces which have a slight concavity, often crossed by a faint longitudinal ridge, between the bases of the neural arch and the rib. The neural arches of these vertebræ have a small neural canal, very long narrow pedicels, and zygapophyses which do not project at all laterally, so that the extreme width across them does not markedly exceed the width of the neural arch at the same height in any other portion of its length.

The dorsal vertebræ have centra somewhat constricted in the middle with almost circular articular ends. They are never carinated on the ventral surface. The transverse processes are placed high up and project strongly and somewhat upwards The caudals appear hexagonal in end view, have concave sides both above and below the rib, and a concave hæmal surface sharply marked off by conspicuous ridges. All Plesiosaurs with a vertebral column of this type have small, often very small heads, and a long neck with more than thirty-five vertebræ, the back of about twenty-four vertebræ being comparatively short.

The more important known forms of this series are :—

" *Plesiosaurus conybeari* " Sollas. Lower Lias.   England.
Microcleidus sp. div. ... . Upper Lias. England.
Murænosaurus sp. div. ... . Oxfordian. England.
Colymbosaurus sp. div. ... . Kimmeridgian. England.
Elasmosaurus sp. div. ... . Lower and Upper Cretaceous.
                                     Europe, N. America, Australia.

That these forms are actually genetically related is shown by a comparison of many other qualities, which may be found in the pelvis, and indeed in the details of the structure throughout. The comparable series of shoulder-girdles and fore-limbs described in this paper afford still further grounds for assurance.

I know further remains, though only fragmentary, of the same type from the Middle Lias, Great Oolite, Portlandian,

and Lower Greensand of Britain, so that the continuous occurrence of the group in Europe throughout its history is certain.

It must be realized that there are not only a large number of individual types of Plesiosaurs which do not belong to this series, but that several similar series, one at any rate restricted to brackish water, are suggested by known material. There is in fact no group of animals which would more fully repay the labour and travel involved in the production of a complete monograph.

THE NOTHOSAURIAN SHOULDER-GIRDLE AND FORE-LIMB.

The structure of the Nothosaur shoulder-girdle and humerus was very accurately described by H. v. Meyer. 'Zur Fauna der Vorwelt,' pt. ii., Frankfort, 1847. The structure of the more distal parts of the limb, not yet completely known in *Notho-saurus*, is well illustrated in the smaller forms *Lariosaurus* and *Pachypleura*, which have an essentially similar structure.

The structure of the shoulder-girdle will be more readily understood from text-fig. 2 than from a lengthy description. The important features are :—

1. The fact that the coracoids meet in a symphysis.
2. That each coracoid is enlarged and directed backwards and inwards from the glenoid cavity.
3. The presence of a notch, obviously converted into a foramen during life by an unossified cartilaginous region, which opening is the precoracoid foramen.
4. The comparatively normal scapula with a blade rising above and only slightly in front of the glenoid cavity.
5. The extremely powerful rigid clavicular arch.
6. The sutural union between the clavicle and the acromion.

The humeri of *Nothosaurus* in the British Museum are all imperfect, although one (No. R. 1083 *a*, B.M.N.H.) shows certain muscle-insertions.

A very small humerus (R. 1409) referred to *Conchiosaurus* shows nearly all the areas of insertion of muscles most clearly : so far as they can be compared these agree with those shown in the other specimens available. The humerus is represented from four aspects in text-fig. 3. The areas of insertion of the coraco-brachiales indicated in dotted lines in these figures are inserted from a *Nothosaurus* humerus in which they are vividly shown.

The Nothosaur humerus is a powerful, somewhat bent bone with a proximal end a little thicker dorso-ventrally than antero-posteriorly and a dorso-ventrally flattened and widened distal end. The sudden bend in the anterior margin marks the meeting place of the insertions of the deltoid and pectoral muscles, the former having an attachment along an oblique

ridge on the anterior face of the bone, and the latter along the ridge forming the anterior margin.

There is a distinct insertion of the scapulo-humeralis anterior along a ridge lying parallel to and proximal of the deltoid insertion.   There is no evidence of any scapulo-humeralis posterior.

On the caudal surface of the bone, not far from the head, is a well marked roughening, which appears to represent the attachment of the subscapularis muscle.

On the dorsal surface at the extreme posterior edge, at a point corresponding to the similar insertion of the pectoralis, is the place of attachment of the M. latissimus dorsi.

On the ventral surface of the humerus not far removed from the head are well marked insertions for the supracoracoideus and the subcoracoideus.

Text-figure 2.
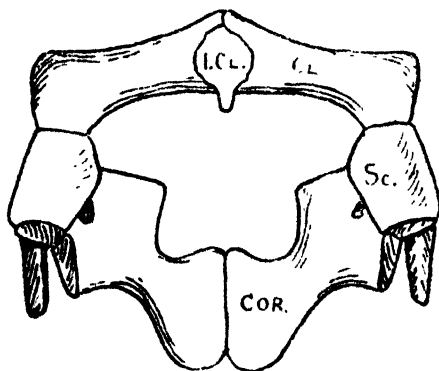
Shoulder-girdle of *Nothosaurus*, from the ventral surface. Cl., clavicle; Cor., coracoid ; I.Cl., interclavicle; Sc., scapula. After Williston.

Finally, the humerus of *Nothosaurus* referred to above gives very clear evidence of a large oval insertion lying in the middle of the ventral surface in the proximal third of the bone, which can only be for the M. coraco-brachialis brevis ; and a more irregular insertion of the M. coraco-brachialis longus occupying a considerable portion of the more distal part of the ventral surface.

Nothosaurus has a forearm which is short in comparison with the humerus and seems to have been carried in the same straight line as that bone, the elbow-joint not being bent and apparently capable of little motion.

Its remains are always found in marine rocks (*i. e.* the Muschelkalk) which are shallow-water, inshore deposits, none having ever been found in the open-sea deposits of the American Trias, which are so rich in Ichthyosaurs.   Thus, although

predominantly aquatic, it is not a pelagic animal, an inhabitant of the wide oceans such as the later Plesiosaurs became.

When used for swimming the fore-limb of the Nothosaurs must have been carried extended at right angles to the principal plane of the animal with its broad faces vertical; it then forms a paddle.

The probable insertions on the body of the muscles which moved it, and the motions to which they gave rise are as follows:—

GROUP A. Muscles moving the distal end of the humerus forward.

The Deltoid probably arises from the whole length of the clavicle and the interclavicle. Draws the whole bone forwards, and in the absence of any similar muscle inserted on the caudal edge of the humerus does so with the broad plane of the bone horizontal.

GROUP B. Muscles moving the outer end of the humerus backward.

1. The Coraco-brachiales brevis and longus arise from the admedian part of the lower surface of the coracoid. They pull the humerus backward and downward and do not tend to rotate it.

2. The Subcoracoideus arises from the visceral surface of the coracoid. Pulls the humerus backward and tends to rotate its anterior edge upwards.

The Supracoracoideus arises from the ventral surface of the coracoid. Pulls the humerus backward and tends to rotate its anterior margin downwards. Its rotatory action is greater than its swimming effect.

3. The Pectoralis arises from the ventral part of the belly, i. e. from the abdominal ribs. Pulls the humerus backward and tends to rotate its anterior margin downwards.

The Latissimus dorsi arises from the dorsal part of the trunk. Pulls the humerus backward and tends to rotate the arm so that its anterior edge moves upwards.

All these muscles thus pull the humerus backward, their joint action giving the powerful stroke required for swimming. The forces tending to rotate the humerus balance one another, the subcoracoideus acting in the opposite sense to the supracoracoideus and the pectoralis to the latissimus dorsi.

There remains the force driving the humerus ventrally, arising from the action of the coraco-brachiales; this is opposed and balanced by the action of the scapulo-humeralis anterior and the subscapularis, arising from the outer and visceral surfaces respectively of the dorsal part of the scapula.

Thus the musculature permits of a very powerful backward stroke of the arm, resulting in a forward motion of the animal,

and of much less intense movements in all other directions, the forward motion of the paddle in the feathered position, *i. e.*, with the broad plane horizontal, being directly brought about by the deltoid.   Backing water is only possible by drawing the humerus forward by the deltoid and retaining it in a swimming position by the action of other muscles which are in the main opposed to it, so that it is probable that the animal was not capable of quick turning by backing water with one paddle and going ahead with its fellow.

Text-figure 3.
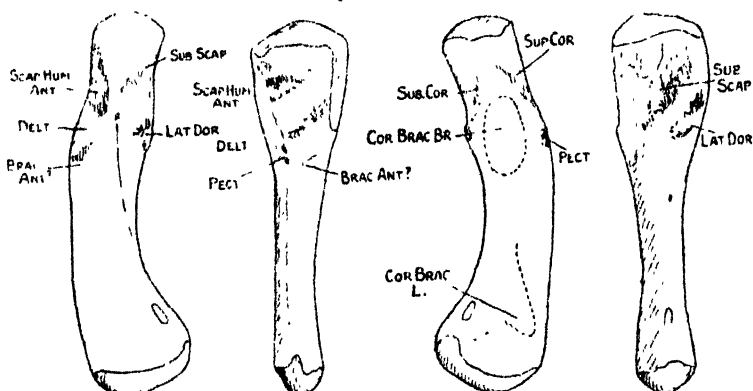
Left humerus of a Nothosaur ? *Conchiosaurus.*   Dorsal, anterior, ventral, and posterior views.

Brac.Ant., insertion of M. brachialis anticus; Cor.Brac.Br., M. coraco-brachialis brevis; Cor.Brac.L., M. coraco-brachialis longus; Delt., deltoid. Lat.Dor., M. latissimus dorsi; Pect., pectoralis; Scap.Hum.Ant., scapulo-humeralis anterior; Sub.Cor., subcoracoideus; Sub Scap., subscapularis.

Even the most primitive known Plesiosaurs differ considerably from the Nothosaurs in their shoulder-girdles and fore-limbs. On the whole the classical *Plesiosaurus dolichodeirus* Cony. is one of the most primitive known ; it is described here because a pair of exquisitely preserved humeri in the Manchester Museum show all the muscle-insertions most clearly.   It is not a member of the Elasmosaur series, but is in its structure very close to " *P.*" *conybeari*, the basal member of that phyletic line.

PLESIOSAURUS DOLICHODEIRUS Conybeare.

The shoulder-girdle of *P. dolichodeirus* is well known ; the ventral surface of this region in R. 1315 B.M.N.H. has been figured by Woodward and Andrews, and may have formed the subject of one of Owen's figures.   A more recently acquired specimen in the Museum shows the dorsal surface of the coracoids, and isolated scapulae add to our knowledge of its structure.

The coracoids are large, meeting in median suture from a point well in advance of the glenoid cavity to their posterior ends. The posterior part of the bone is narrow, the postero-lateral corner not being thickened and produced into a process as it is in many later forms.

The scapula consists of a trihedral rod, articulating with the coracoid and forming the front of the glenoid cavity, and extending forward and inwards on the ventral surface of the animal at about 45° to the axis of the animal. The dorsal ramus rises from the upper surface of this rod considerably in advance of the glenoid cavity as a narrow plate of oval section, which reaches up and backward for a considerable distance over the pectoral ribs. The anterior end of the scapula widens so that it approaches, and in very aged individuals even meets, the anterior extremity of the coracoid near the middle line. This widened extremity underlies the clavicle, whose pointed lateral end is received in a depression on the dorsal surface of the bone near the root of the dorsal process.

The clavicles and interclavicles are united by close inseparable sutures so as to form a curved plate of bone. The clavicle articulates with the dorsal surface of the scapula, and widens from there towards the middle line, terminating in the long suture with the interclavicle, its extreme inner posterior corner being underlain by the front of the coracoid.

The interclavicle is a flat bone rising posteriorly into a median ventral ridge which is received in a special V-shaped depression formed by the two coracoids. The anterior edge of the bone is cut out into a wide median notch, bounded on each side by roughened projections which form the most anterior points of the girdle.

Humerus.

The humerus is a relatively massive bone. The head is deeper in a plane at right angles to the broad plane of the distal end than it is wide. The main, nearly hemispherical articular head is continued upwards by an extension onto the "trochanter"; this extension serves to articulate with the anterior part of the glenoid cavity, i. e. that part formed by the scapula, when the bone is in the swimming position with the broad plane vertical.

In the middle of its length the shaft of the bone is much flattened, being nearly twice as wide as deep. The distal end of the bone is widened, but only slightly so in comparison with many later forms: it bears the usual two faces for the radius and ulna, and in addition a small facet for a "postaxial" bone. It is an interesting and unique feature that the ventral surface of the distal end of the bone is concave, not as in later types convex, so that the paddle as a whole is slightly spoon-shaped, a simple adaptation leading to better holding of the water.

Owing to a sudden change in the direction of the anterior margin at one third of the length from the proximal end, the whole bone appears bent ; at once recalling the Nothosaur

Text-figure 4.
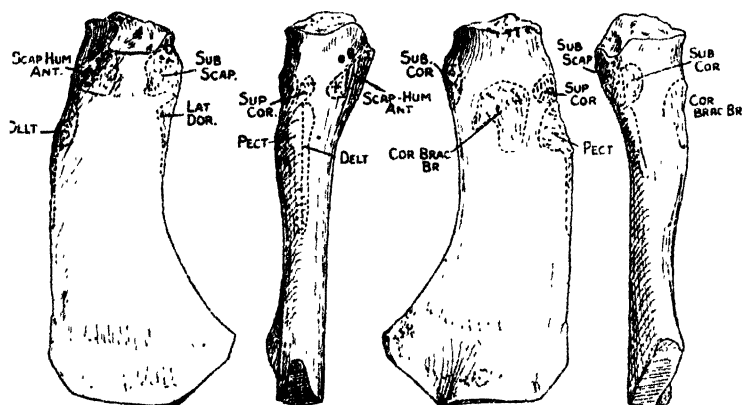
Left humerus of *Plesiosaurus dolichodeirus* Conybeare. Dorsal, anterior, ventral, and posterior views. Reference letters as in text-fig. 3.

humerus. Very near the distal end the anterior margin is notched, presumably by a representative of the ectepicondylar foramen.

Musculature.

The sudden bend in the anterior margin of the bone marks the proximal end of the insertions of the deltoid and pectoral muscles. The pectoralis has a large roughened attachment lying on the lower surface and front edge of the bone and extending outward for about a quarter of its length. The deltoid has a similar but much smaller and less distinct insertion on the upper surface near the anterior margin.

There is a well-marked insertion of the M. scapulo-humeralis anterior on the upper surface and the anterior face of the thickened head of the bone.

The subscapularis has a similar insertion on the upper surface just below the head near the posterior margin.

A roughening of the posterior margin for nearly half its length represents the insertion of the latissimus dorsi.

On the ventral surface posteriorly is a small attachment for the subcoracoideus, confluent over the posterior margin with that of the subscapularis.

The whole of the middle of the lower surface of the humerus for one third of its length is occupied by the enormous insertion of the coraco-brachialis brevis.

Finally, there is an area faintly distinguishable from that for the coraco-brachialis, lying just proximal to the pectoralis insertion for the supracoracoideus.

It is probable that an insertion running as a strip across the distal part of the lower surface of the humerus is for the coraco-brachialis longus.

A series of indistinguishable insertions on the lower surface near the distal end and on the posterior margin represent the flexors which prevent over extension of the forearm and hand.

The character of the articulations between the elements of a Plesiosaur limb shows that the whole formed a rigid or nearly rigid paddle enclosed within a bag of skin like a whale's flipper. There is slight evidence that the distal part of the paddle was broader than would appear from the skeleton, the posterior edge being extended and supported on an unossified skeleton as it is in the somewhat similar limb of the Ichthyosaurs. Comparison with the whales suggests that the muscles associated with the distal parts of the limb had undergone much reduction, being in all probability represented solely by ligaments or disappearing entirely.

Although the shoulder-girdle bones which I have examined do not show satisfactory evidence of muscle-insertions, it is possible from a consideration of their shapes and of the humerus to be reasonably certain of the general distribution of the musculature; consideration of later forms lends confirmation to the following reconstruction.

The girdle as a whole must be held in place by a muscle or muscles arising from the neck and inserted on the anterior edges of the scapulæ, clavicles and interclavicle; roughenings for their insertions are often well-marked. There must also be serrati arising from the ribs in the pectoral region and inserted on the visceral surface of the dorsal ramus of the scapula. Finally, there was undoubtedly some muscle attached to the coracoid and passing backwards to the abdomen in order to take forward thrusts of the girdle. When swimming the paddle was held with the broad plane vertical and the ulnar edge upwards.

Described under the same heads as those of Nothosaurs, the muscles moving the humerus are as follows:—

GROUP A. Muscles moving the outer end of the humerus forward. (For insertions see figures and description of the humerus.)

    1. The Deltoid probably arises from the whole exposed area of the clavicle and interclavicle and the dorsal part of the scapula. Draws the whole bone forward and tends to rotate it so that the broad plane becomes horizontal.

    2. The Scapulo-humeralis anterior probably arises from the ventral surface of the anterior ramus of the scapula. Draws the humerus forward and tends to rotate its anterior edge upward.

    3. The Subscapularis probably arises from the upper surface of the anterior ramus and the dorsal ramus of the scapula. Tends to draw the humerus forward and to rotate its anterior edge downward.

The two latter muscles thus combine to draw the humerus forward without rotating it, and enable the animal to turn by backing water with one paddle whilst going ahead with the other. This action of these muscles is dependent on the shift forward of the part of the scapula on which their insertions lie to a point well in advance of the glenoid cavity ; the lengthening of the posterior ramus of the scapula, a feature which is characteristic of the Plesiosaurs and entirely peculiar to them, is necessary to allow the subscapularis to pass round from its origin on the visceral surface of the anterior ramus of the scapula to its insertion on that face of the head of the humerus which is anterior when the bone is in the swimming position.

Group B. Muscles moving the outer end of the humerus backward.

1. The Coraco-brachialis brevis (and longus, if present) arise from the admedian part of the ventral surface of the coracoid and from the hinder end including the postero-lateral corner. Pulls the humerus backward in the swimming position, and does not tend to rotate it.

2. The Subcoracoideus arises from the visceral surface of the coracoid ; it not only draws the limb as a whole backwards but tends to rotate it, moving its front edge upward.

3. The Supracoracoideus must have arisen from part of the ventral surface of the coracoid ; its action is not applied to the bone in a mechanically efficient way, but it tends to draw that bone backward and downward and to rotate its front edge downward.

4. The Pectoralis arises from the belly and draws the humerus backward, tending to rotate its front edge downward.

5. The Latissimus dorsi arises from the dorsal part of the trunk ; it pulls the humerus backward and tends to rotate its front edge upward.

The five muscles listed above in combination give the powerful backward stroke required for swimming, and the two pairs of muscles balance one another so that the rotation which would ensue from the action of any one of them alone is prevented by the action of the other member of the pair.

The humerus tends to be depressed by the action of all the muscles arising from the body below the glenoid cavity and raised by those which arise from the dorsal part of the scapula and trunk. The muscles serving to depress the humerus act at a considerable mechanical disadvantage owing to their oblique insertion on the humerus, and can thus be counterbalanced by the comparatively less powerful muscles opposed to them which have a more favourable insertion.

The great differences between the shoulder of a Plesiosaur such as *P. dolichodeirus* and that of a Nothosaur which represents

its morphological ancestor are susceptible of a mechanical
explanation, which also accounts for those features in which the
Nothosaur shoulder-girdle differs from that of a more ordinary
reptile.

Text-figure 5.
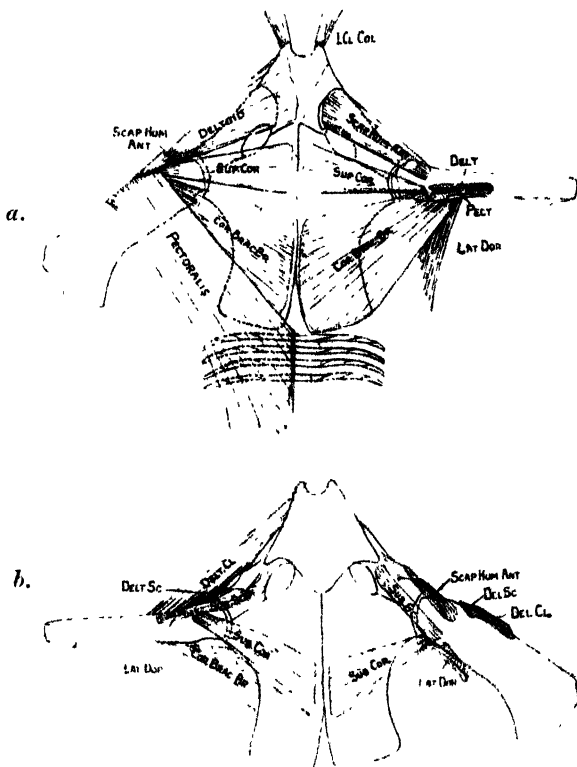
Shoulder-girdle and humeri of *Plesiosaurus dolichodeirus* with a reconstruction
    of the musculature. The right humerus is in the feathered position, the
    left in position for the swimming stroke.

a. Ventral aspect, deltoid and pectoralis cut short on the left side.

b. Dorsal aspect, latissimus dorsi cut short on both sides, the deltoids on the
    right.

Reference letters as in text-fig. 3.

The Plesiosaurs are completely aquatic, and in consequence
gain the whole support necessary from flotation. The limbs
are therefore freed for use exclusively as paddles serving for
propulsion and for steering. It has already been pointed out that
the plesiosaur limb is essentially a rigid oar. In discussing the
mechanics of such an oar it must be borne in mind that the
distal end is the fixed point, the fulcrum.

The muscles concerned in the swimming stroke, *i. e.* direct backward pull of the humerus, fall into two groups :—

    a. Those connected with the limb and with the coracoid: M. coraco-brachialis and M. subcoracoideus.

    b. Those connected with the limb and with the trunk : M. latissimus dorsi and M. pectoralis.

Analysis of Stresses developed by contraction of Muscles of Group a in the Shoulder-girdle. (See text-fig. 6.)

These muscles may be diagrammatically considered as arising from the postero-lateral corner of the coracoid and being inserted on the middle of the shaft of the humerus.

Text-figure 6.
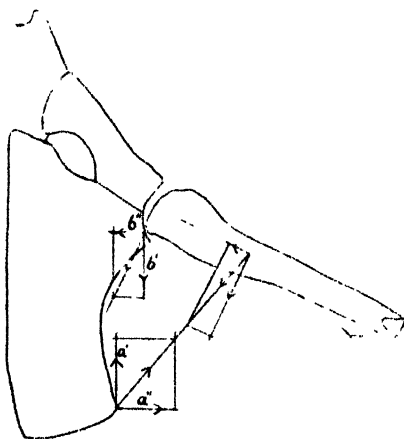
Diagram to explain the forces acting on a plesiosaur shoulder-girdle, described in the text.

The actual force exerted is a tension in the muscle. The stress at the posterior insertion can be resolved into two: a', which tends to drive the whole girdle forward, and a'', which pulls the back of the coracoid outward.

The stress at the humeral insertion may be resolved into a force at right angles to the bone which tends to move it backwards, and an inward thrust along the axis of the bone which forces the head of the humerus into the glenoid cavity. Leaving this thrust out of consideration, the force between the head of the humerus and the glenoid cavity is a thrust, backward and inward. This can be resolved into two forces, b' tending to drive the coracoid backward, and b'' directed inward. The point of application of b' being further from the fulcrum than that of a', b' must always be smaller than a', so that there is a resultant

force tending to drive the girdle forwards. The result of all the other forces is a compression of the coracoid between the glenoid cavity and the middle line, and a couple tending to turn the girdle so as to separate the posterior ends of the coracoids.

Muscles of Group B having no insertion on the coracoid produce stresses in the girdle only at the glenoid cavity, which resolve exactly as do those of Group A.

As a total result, muscles of Group B tend to drive the girdle as a whole backward and to produce a compression between the glenoid cavities.

If we sum the effects of the two classes of muscles we find that there are left only the following forces :—

1. A force tending to drive the girdle forward, whether positively or negatively depending on the relative strengths of the muscles of types A and B. This force may be zero, and in any case will be comparatively small.

2. A compression between the glenoid cavities, which will be large as it is added to by all the muscles.

3. A couple tending to separate the posterior ends of the coracoids.

The chief force which drives the animal forward is exerted at the insertions of the pectoralis and latissimus dorsi on the trunk, if those muscles are relatively powerful when compared with the intrinsic shoulder muscles.

In so far as the Nothosaur limb is used as a rigid oar the preceding analysis applies to its shoulder-girdle and gives an explanation of certain of its peculiar features.

The lengthening of the coracoid is a direct adaptation to increase the length, and hence the possible energy output and range of action of the coraco-brachialis and subcoracoideus, whose action is shown by the above analysis to drive the animal forward. (A similar need is met in a similar way in *Archæopteryx*.) The coracoid is directed backward so as to improve the mechanical efficiency of the application of the muscle by making its insertion on the humerus more nearly at right angles. The necessity of supporting the great stress developed between the glenoid cavities by the thrusts of the heads of the humeri is the explanation of the symphysis between the coracoids and of the very rigid attachment of the elements of the clavicular arch to each other and to the scapulæ.

The extreme rigidity of the anterior part of the girdle is called for in addition by the fact that compression of it automatically gives rise to a couple opposing the rotation of the coracoids induced by force 3.

The most striking difference between the Nothosaur and the Plesiosaur girdle is the extension forward of the symphysis between the coracoids to a point in advance of the glenoid cavity. This change results in the production of a bar of bone, which is actually very much thickened, between the glenoid cavities, where it takes the great stress developed by force 2

directly, and by its presence relieves the clavicular arch of the greater part of the stresses to which it is subject in the Nothosaur girdle.

The widening of the hinder end of the coracoid is of obvious adaptive significance in that it renders the insertion of the coraco-brachialis on the humerus more nearly at right angles to that bone when it is extended normally to the animal's principal plane; this angle of insertion increases the resultant backwardly directed force relatively to the inward thrust along the axis of the bone.

The extension forward of the scapula and the production of the elongated posterior or glenoid ramus are to be explained on mechanical grounds as leading to an alteration of the direction of the M. scapulo-humeralis anterior and the M. subscapularis, which renders those muscles capable of drawing the humerus forward in the swimming position. Their insertion close up to the head of the humerus makes these muscles act at a great mechanical disadvantage, but they do afford, even although only in a slight degree, the possibility of backing water with the paddle, a power which must have added greatly to the agility of the animal.

It is to be noted that when backing water the head of the humerus is driven inwards and forward into the glenoid cavity, so that the extension of the articular face onto the tuberosity is pressed against the glenoid end of the scapula.

PLESIOSAURUS CONYBEARI Sollas.

The structure of the shoulder-girdle of *P. conybeari* has been clearly described by Sollas (Q. J. G. S. 1881, vol. xxxvii. p. 440). It is in essentials very similar to that of *P. dolichodeirus*, differing only in the less powerful connection, if indeed there be any contact, between the posterior end of the interclavicle and the anterior end of the coracoids. The scapula has a large dorsal ramus and the anterior ramus is slender, not markedly enlarged on the ventral surface and far removed from the inner anterior end of the coracoid.

The humerus is not very well shown, but recalls that of *P. dolichodeirus* in the width of the shaft in the middle of its length, in the comparatively slight enlargment of the distal end, and in the convex anterior border. No details of the muscle-insertions are shown in the type specimen, but it is in every way probable that the whole musculature was in essentials similar to that of *P. dolichodeirus*.

MICROCLEIDUS.

The shoulder-girdle of the plesiosaurs of the genus *Microcleidus* from the Upper Lias is only shown completely in the great skeleton in the Manchester Museum described by the present writer (Manch. Memoirs, vol. lv., 1911).

The important features are :—

1. The coracoids though large are not greatly widened caudally.
2. The scapulæ have much enlarged anterior rami, so that the two meet in a symphysis and extend backward to unite with the anterior end of the coracoids in the middle line. This condition only occurs in old individuals.
3. The dorsal ramus of the scapula is relatively small.
4. The outer edge of the posterior ramus of the scapula is continued forward by a sharp ridge which divides the horizontal surface from the more vertical surface which is an extension of the outer face of the dorsal ramus.
5. The clavicular arch is reduced to thin sheets of bone adherent to the dorsal surface of the anterior rami of the scapulæ. The interclavicle seems to have vanished completely.

Certain muscle-insertions are visible on the scapula. The inner surface of the extreme dorsal part of the dorsal ramus has a definite insertion for the serrati. The admedian part of the lower surface of the anterior ramus of the scapula has a large

Text-figure 7.
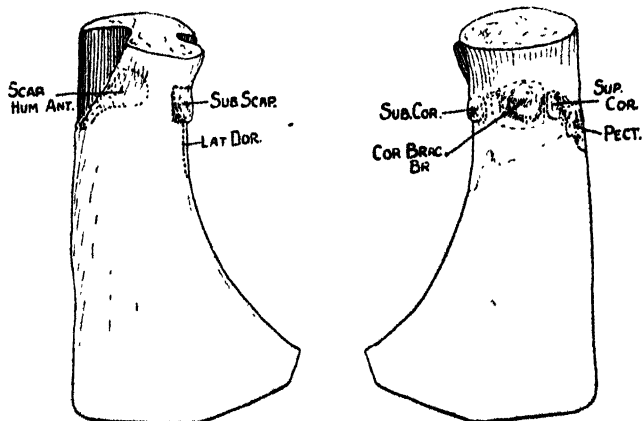
Left humerus of *Microcleidus* sp. Dorsal and ventral view.
Reference letters as in text-fig. 3.

irregular roughening, which appears to mark the place of origin of the M. scapulo-humeralis anterior.

On the dorsal surface the anterior ramus of the scapula and the overlying clavicle show certain roughenings which are apparently muscle-insertions. One of these lying at the anterior part of the root of the dorsal ramus and crossing the bone transversely is probably the attachment of the subscapularis; the others,

which lie entirely on the clavicle, may be for claviculo-cervical muscles homologous with cleidomastoids and sternomastoids.

A pair of humeri of another individual of a different species of *Microcleidus*, also in Manchester, shows all the muscle-insertions very clearly. They will best be understood from text-fig. 7.

The important differences from *P. dolichodeirus* are:—

1st. That the whole group of insertions are concentrated in the proximal third of the bone and do not extend along it.

2nd. That there is no evidence of any deltoid insertion.

3rd. That the insertions for the pectoralis and latissimus dorsi are much smaller than in *P. dolichodeirus* and less strongly marked.

4th. That the anterior edge of the humerus is quite straight, showing no trace of the Nothosaurine bend.

5th. That in the region of the distal end of the muscle-insertions the bone is much thickened and of more circular section.

6th. That the bone is relatively wider distally.

The apparent loss of the deltoid is to be correlated with the noticeable reduction in size of the dorsal part of the scapula, and especially with the fact that as the ventral surface of the clavicular arch is completely attached to the dorsal surface of the anterior ramus of the scapula, there can be no clavicular deltoid, which is probably the important part of the muscle in *P. dolichodeirus*.

MURÆNOSAURUS.

The structure of the shoulder-girdle in several species of the genus *Murænosaurus* from the Oxfordian has been well described by C. W. Andrews ('Catalogue of the Marine Reptiles of the Oxford Clay', British Museum (Natural History), 1910). It varies from species to species, mainly in the age at which a definite degree of ossification is attained, in the slenderness or massiveness of the bones, and especially in the structure of the reduced clavicular arch.

It is certain that *Murænosaurus* is not a descendant of *Microcleidus* itself, because it retains in the relatively large interclavicle a bone already lost by the former genus; the close relationship of the two genera is however certain.

Essentially the shoulder-girdle of *Murænosaurus* is similar to that of *Microcleidus*: it has large coracoids whose postero-lateral corners are only slightly produced. In old individuals these bones reach forward in the middle line to touch the scapulæ. The scapula has an enlarged anterior ramus which extends inwards to reach its fellow and the anterior end of the coracoid. The dorsal ramus of the scapula is relatively much smaller than in *Microcleidus* and lies more nearly in the same plane as the

anterior ramus, from which its outer surface is separated by a strong ridge which extends along the outer margin of the posterior ramus forward.

The clavicular arch consists of an interclavicle which is of some substance (about one centimetre thick), with whose lateral margins the extremely thin remnants of the clavicles articulate; the whole mass lies on the dorsal surface of the scapula, and in old individuals is only visible from below to a very slight extent.

The humerus of *Murænosaurus* differs from that of *Microcleidus* in having a definitely concave anterior edge. The shaft is thicker and more nearly circular in section. The muscle-insertions resemble those of *Microcleidus*, but the pectoralis insertion is even less pronounced.

COLYMBOSAURUS.

The Kimmeridgian plesiosaurs of the Elasmosaur line belong to Seeley's genus *Colymbosaurus*, which has never received proper description or recognition. Existing materials in England demonstrate the presence of two well-marked species—a large form to which the names *Plesiosaurus manselli* Hulke, *P. megadeirus* Seeley, and probably *P. trochanterius* Owen have been applied, and a small form which is at least equally common but does not seem to have received a name—at least none has ever been applied to adequate material.

The two forms differ mainly and very markedly in size, but also slightly in proportions. My account of the shoulder-girdle is founded on the associated and quite perfectly preserved coracoids and a scapula from the Kimmeridge Clay of Shotover, Oxford, now preserved in the Manchester Museum. The determination of these bones depends on the fact that they agree exactly in size and structure with the imperfect remains of the homologous elements in two incomplete skeletons from Ely and Haddenham in the Sedgwick Museum. These specimens retain humeri and other limb bones and cervical vertebræ which are characteristic of the smaller species, and give us the size of the humerus relative to the shoulder-girdle in this species. My account of the humerus is mainly drawn up from isolated bones of the large form (*C. manselli*) in the Manchester Museum.

Text-fig. 8 is, however, drawn from a bone of the small species, which is less advanced in structure than the larger form.

Of the shoulder-girdle only the scapulæ and coracoids are known in *Colymbosaurus*. The coracoids are short and extremely massive, the thickened ridge between the glenoid cavities being remarkably powerful. The lateral border is throughout thickened and is produced into special outwardly turned posterior angles. The anterior end of the coracoid in the middle line is produced forward to meet the scapula. The

scapula shows scarcely any trace of its original triradiate shape, it is a nearly flat sheet of bone recalling a pointed shovel. The glenoid end is comparatively slender, and is connected with the main mass of the bone by a narrow neck. The dorsal and anterior rami are confluent, distinguished from one another only by a strong straight ridge dividing the ventral surface into two nearly equal portions. The ridge is homologous with the outer margin of the anterior ramus of the *Plesiosaurus* scapula. The actual dorsal projection is placed very far forward and is of very small size, being thin and weak in consonance. In adults the anterior ramus meets its fellow and passes backward to the coracoid. In *Colymbosaurus* the division of the humerus into a cylindrical proximal shaft and a flattened expanded distal end, lens-shaped in section, is strongly marked. The anterior border is concave.

Text-figure 8.
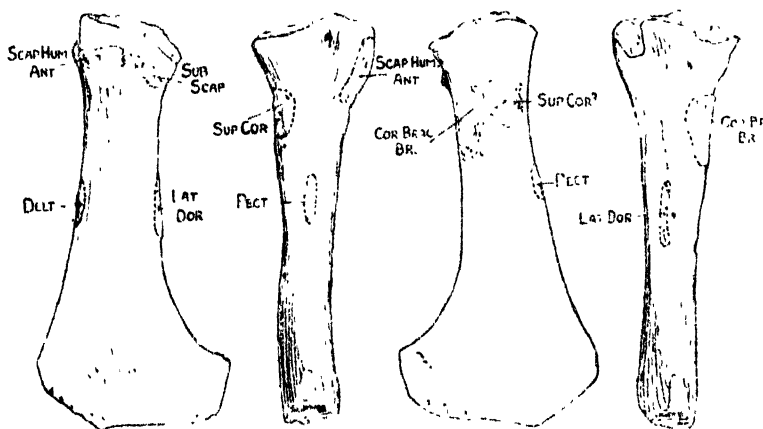
Left humerus of *Colymbosaurus* small species.
Reference letters as in text-fig. 3.

That anterior face of the proximal part of the shaft which passes into the anterior edge of the flattened end is quite flat, supporting a very small insertion for the pectoralis and deltoid muscles in the small form ; in most, perhaps in all individuals of the large form no trace whatsoever of these muscles can be seen. The insertion of the latissimus dorsi is feebly represented in its normal position on the posterior margin. There are large, very proximally placed insertions of the scapulo-humeralis anterior, the supracoracoideus, coraco-brachiales, subcoracoideus, and subscapularis, which agree with those of *Muranosaurus* and, indeed, of *Microcleidus.*

The humerus of *Colymbosaurus* articulates distally with three bones—the radius, ulna, and a third bone which may be the

pisiform, but which in the absence of any naturally articulated
carpus cannot really be determined. The radius and ulna are
extraordinarily short, especially in the large form.

ELASMOSAURUS.

I have never been able to handle well-preserved *Elasmosaurus*
pectoral-girdle and limb bones, and am hence dependent on
figures and descriptions for the following account of its structure.

Text-figure 9.
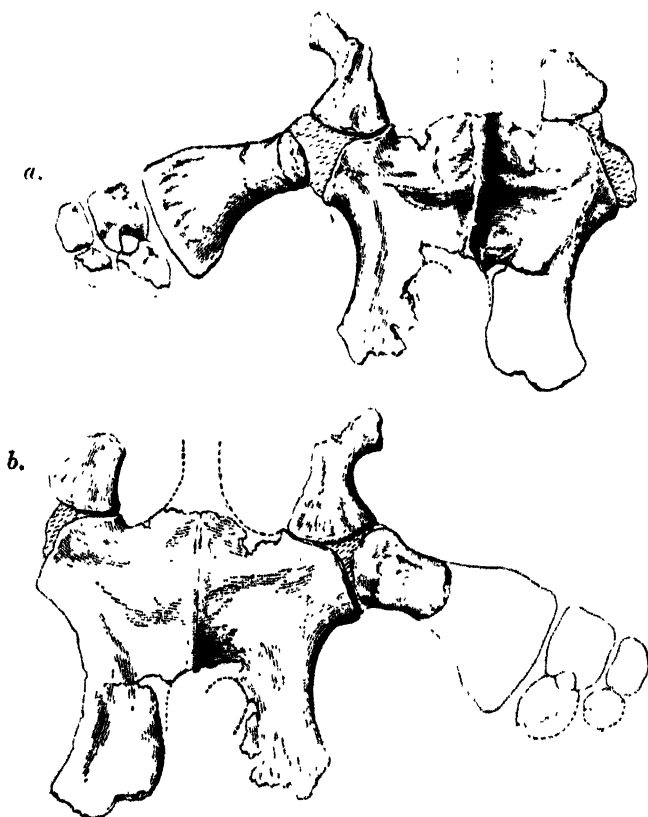
Elasmosaurus serpentinus Cope. From the type specimen.
Pectoral girdle and right limb.
a. Ventral surface. *b.* Dorsal surface.

The clavicular arch is not known. The coracoids are short, sepa-
rated from one another posteriorly by a gap and without a produced
postero-lateral corner. In the type-specimen of *E. platyurus*,

which is obviously an old individual, Cope represents the scapula as an enormous flat sheet of bone nearly equal in size to a coracoid, with a short ill-defined laterally directed process representing the dorsal ramus. In the very similar *E. serpentinus*, as shown in drawings (text-fig. 9) which I owe to the American Museum and Dr. Gregory, there is shown on the ventral surface of the scapula a ridge exactly similar to that in *Colymbosaurus*. Other Elasmosaur shoulder-girdles (*E. snowii* and *E. marshi*) figured by Williston and Riggs, differ in the smaller size of their anterior rami, which sometimes do not even meet each other, and in their more definite dorsal rami; these differences are obviously due to the youth of these individuals.

The humerus of *Elasmosaurus* is an extremely short bone, with a rounded head and a concave anterior border, which articulates with two bones only distally. Nothing is known of the muscle-insertions. The fact that the humerus only supports two bones, shows that *Elasmosaurus* is not actually a descendant of *Colymbosaurus*, although the two forms are closely connected. *Colymbosaurus* may probably be a direct descendant of *Murænosaurus*, which genus itself is of unknown ancestry. *Microcleidus* represents a somewhat aberrant, precociously advanced near relative of the Murænosaur ancestor. *Microcleidus* may perhaps be an actual descendant of *P. conybeari*.

Text-fig. 10 represents the ventral aspect of the shoulder-girdles, humeri, and forearms of the five forms reduced to the same absolute width across the glenoid cavities, and arranged in their correct time order. Omitting from consideration *P. conybeari*, this series shows the following changes progressing regularly, each stage showing an advance on that before it :—

1. The coracoid gets steadily smaller in area and shorter.
2. The anterior part of the scapula becomes larger throughout the series.
3. The scapulæ become gradually converted into flat bones.
4. Up to *Colymbosaurus* the postero-lateral corners of the coracoids become thicker and more pronounced.
5. The humerus steadily becomes relatively shorter.

Except in the case of those numbered 4 and 5, the changes between *P. conybeari* and *Microcleidus* are in the same direction as those between *Microcleidus* and *Murænosaurus*. The individual of *Microcleidus* from which the figure is drawn is unusual in the genus in the exceptional length of its humerus, and perhaps also of its coracoids. I use the figure because it represents the only known shoulder-girdle which is satisfactorily preserved: it is probable that with a more usual form *Microcleidus* would show changes in the same direction as the rest of the series.

Text-fig. 11 represents lateral aspects of the shoulder of a series of forms reduced to the same absolute length and arranged in correct time order ; no such figure of *Elasmosaurus* is available,

Text-figure 10.
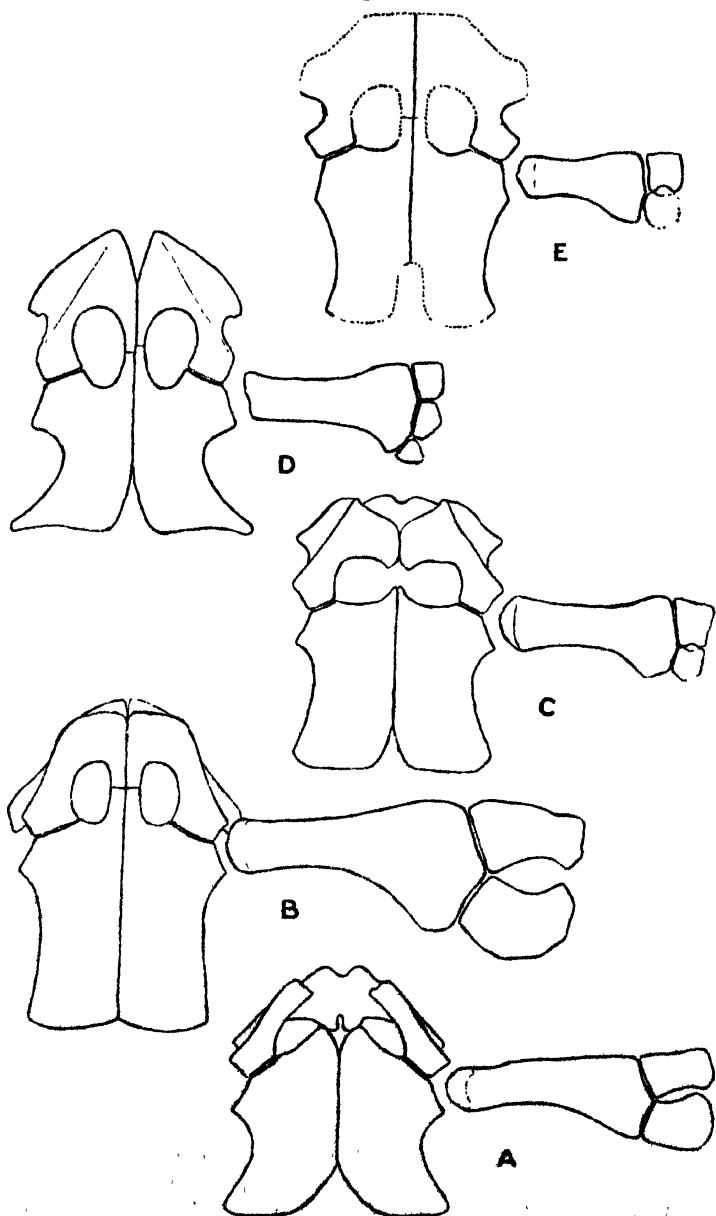
Series of shoulder-girdles and left paddles of Elasmosaurids.

A. *Plesiosaurus conybeari* Sollas. B. *Microcleidus homalospondylus* (Owen).
C. *Muraenosaurus* sp. D. *Colymbosaurus* small species. E. *Elasmosaurus* sp.

so that the last term of the series is missing.   Existing material of *Plesiosaurus conybeari* not allowing of the production of a suitable figure, its place is taken by *P. dolichodeirus*, which has a similar structure.

Finally, a figure of *Nothosaurus* is introduced as a first term.

Text-figure 11.
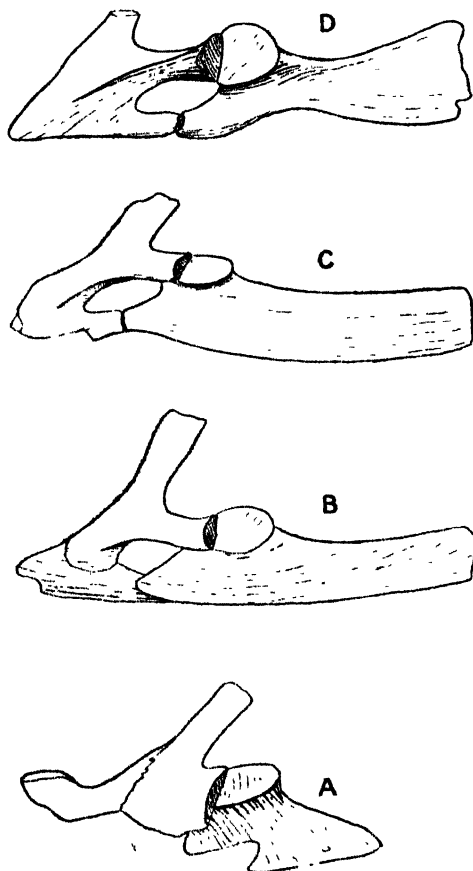
Plesiosaur pectoral girdles from the left side.
A. *Nothosaurus* sp.   B. *Plesiosaurus dolichodeirus* Cony.
C. *Microcleidus homalospondylus* (Owen).   D. *Colymbosaurus* sp.

On account of the exceptional length of the coracoid in the individual figured, *Microcleidus* does not show so good an intermediate structure between *Plesiosaurus* and *Muraenosaurus* as would be expected from a more normal specimen.

This series shows the following additional progressive changes :

6. The dorsal ramus of the scapula is steadily reduced in size.
7. The dorsal ramus of the scapula steadily travels forward from the glenoid cavity.

The discussions of the musculature of individual forms included in the text furthermore bring out the following changes, which are again progressive, each form showing an advance on that which precedes it : —

8. The deltoid is reduced, and in certain specimens of *Colymbosaurus* vanishes.
9. The pectoral is reduced and vanishes in certain specimens of *Colymbosaurus*.
10. The latissimus dorsi is greatly reduced.
11. The scapulo-humeralis anterior and the subscapularis are carried forward onto the exaggerated anterior ramus of the scapula and converted into muscles whose function is to draw the humerus forward, thereby enabling the animal to back water.
12. The coraco-brachialis longus becomes unrecognisable.
13. All the insertions of shoulder-muscles on the humerus become restricted to the proximal part of the bone.
14. The distal end of the humerus becomes symmetrical about its broad plane.

Discussion of the Mechanical Meaning of the Series of Changes recorded above.

The amount of work which can be performed by a muscle is a function of the area of certain surfaces in the muscle-fibres. Thus, supposing that the diameter of the fibres and their structure remain the same, the possible energy output of a muscle will not depend on the arrangement, but on the volume of the whole muscle.

The possible amount of contraction depends on the length, while the force it can exert varies as its transverse sectional area. Thus, by varying the shape of a muscle without altering its volume, it is possible to increase the force exerted whilst decreasing the distance through which the insertion is moved.

No complete naturally arranged paddles of *Colymbosaurus* and *Elasmosaurus* are known, but there is no reason for supposing that the reduction in size of the humerus in these genera is associated with a similar shortening of the whole limb; such evidence as is available, *e. g.* the paddles figured by Riggs, tends to show that the Elasmosaur paddles were proportionately large.

The gradual concentration of the insertions of the shoulder-muscle and the loss or great reduction of those more superficial muscles whose insertions are more distal, lead to a reduction of the size of that muscle-mass which, in early forms, projects round the base of the limb and spoils such imperfect stream-line form

as the body has. The shortening of the humerus has the effect of converting as much as possible of the exert part of the limb into a flattened paddle, arising from the body with only a very short unflattened region, whose retention is necessary to allow of the rotational movements necessary for feathering.

The experience of all marine tetrapods, whales, ichthyosaurs, etc. shows that this is the best possible approach to the ideal shape for a paddle.

Thus it is probable that in *Elasmosaurus* the flattened paddle rose directly from the uniformly curved body-surface.

Shoulder-muscles whose attachments to the humerus lie close up to the head act at a greater mechanical disadvantage than those with a more distal insertion, so that to secure that the same force can be applied to the distal end of the limb, assuming that its length remains constant, the area of the transverse section of the swimming-muscles must be increased, if their angle of insertion remains the same. In the case of the muscles under consideration the angle which they make with the humerus is altered, becoming much more nearly perpendicular to the long axis of the limb when held out at right angles to the body as the insertions move up to the head. The maximum angle of insertion of any part of the coraco-brachialis brevis on the humerus in *Plesiosaurus dolichodeirus* is about 45° with the limb at right angles to the body, whilst in *Colymbosaurus* it is about 70 . Thus in *Colymbosaurus*, although the swimming-muscles act at a greater mechanical disadvantage in one way, they are more efficiently applied in another. The increase of efficiency in this direction is not however large enough to balance the increased disadvantage due to the shifting of the insertions, so that to secure the development of the same force a muscle of greater cross section is necessary. In *Colymbosaurus* the production of the postero-lateral corner of the coracoid and the excavation of the ventral surface of that bone afford space for the development of such an enlarged muscle.

Although the force drawing the arm backward in Plesiosaurs becomes greater as the angle of insertion of the swimming-muscles approximates more nearly to a right angle, this increased force is only capable of moving the limb through a proportionately smaller arc.

In the Elasmosaurid series the increase in mechanical disadvantage due to the approximation of the muscle-insertions to the head of the humerus is greater than the increase in efficiency due to their more favourable angle of insertion; hence that resultant of the force exerted which tends to drive the animal forward is reduced and accordingly the range of motion of the limb is increased, the work done remaining constant.

In a similar way the nearness of the muscle-insertions to the head increases the rapidity of motion of the paddle if the muscles contract at the same rate. Thus *Colymbosaurus*, by a comparatively slight increase in the size of the muscles coupled with the

alteration in their insertion (passing from the coracoid to the humerus), gains a longer, more rapid and equally forceful swimming stroke together with a more accurately stream-lined form.

As a matter of fact, if throughout the Elasmosaur series the coracoid retained its original length the arc through which the arm could be moved would be of impracticable magnitude: in consequence the coracoid shortens so as to shorten the muscles, which does not decrease the force exerted, but reduces the range of action.

In the Elasmosaur series the pectoralis, which is an important swimming-muscle in the early forms, vanishes probably in association with the moving up of the muscle-insertions toward the head of the humerus. The energy supplied by it has therefore to be made up by increase in the volume of the coraco-brachialis and subcoracoideus. It is impossible to determine whether this result is actually attained. The analysis of the forces acting on the shoulder-girdle given on p. 898 shows that with the disappearance of the pectoralis the girdle as a whole is urged forward during swimming; this motion must be resisted by powerful muscles passing from the coracoid to the belly, as the great reduction of the dorsal ramus of the scapula shows that muscles of the serrati series are not extensively developed.

The foregoing analysis gives an account of the mechanical changes involved by the structural modifications, 1, 4, 5, 9, 10, 12, and 13.

The enormous development of the anterior ramus of the scapula and the conversion of that region into a flat plate is an adaptation to allow of a powerful forward stroke, by the action of the scapulo-humeralis anterior and the subscapularis; as has already been pointed out on page 905. The steady passage forward of the dorsal ramus of the scapula, change 7, resulting in the formation of a long glenoid ramus is necessary to allow of the passage of the large subscapularis from its origin on the inner face of the anterior ramus of the scapula to its insertion on the humerus.

Thus the later Elasmosaurs have the power of making powerful backing strokes with the fore-limbs.

The great reduction of the dorsal ramus of the scapula, the loss of the deltoid, and the great reduction of the latissimus dorsi, show that the later Elasmosaurs have very little power of raising or depressing their fore-limbs—have, in fact no arrangements for rolling over in the water, and must have moved their paddles quite horizontally. Lack of this power, which, when applied, tends to slide the shoulder-girdle round the ribs, allows of a reduction of the dorsal part of the scapula, one of whose main functions is to give attachment to serrati and other muscles which exist in most reptiles to prevent such motion.

Backward motion of the shoulder-girdle on the trunk, which

tends to be produced by backing water, must have been prevented by muscles homologous with cleidomastoids passing from the base of the neck to the anterior border of the scapulæ and the remnants of the clavicular arch. Retention of a representative of the latissimus dorsi is necessary in order to have some muscle to oppose that small force due to the coraco-brachialis which tends to depress the humerus.

Finally, the complete identity in shape of the two broad surfaces of the distal end of the humerus and of the outer part of the limb as a whole is necessary to secure an efficient shape of paddle for use, not only in swimming ahead, but also in backing.

It is thus possible to provide a simple mechanical interpretation of the whole series of fourteen changes in the shoulder-girdle and fore-limb of the Elasmosaur series which can be observed to progress regularly throughout the history of that "lineage."

These changes result in an increased efficiency in swimming and in the development of a powerful backing stroke. The obvious and only probable use of a power of backing water is to secure the power of suddenly turning sideways.

All the members of the Elasmosaur line have small heads and long necks, the number of cervical vertebræ being :—

"*Plesiosaurus*" *conybeari*	35
Microcleidus	39–40
Murænosaurus	42
Colymbosaurus	42+
Elasmosaurus	76

As the individual middle cervical vertebræ are themselves elongated, the length of the neck really exceeds that suggested by the already enormous number of bones.

Long-necked animals of this type do not conform at all closely to the ideal stream-lined form of a body designed to move through a fluid with as little resistance as possible. This shape is very accurately attained by fish and especially by Whales. Even long-snouted forms like Dolphins and Ichthyosaurs make very close approaches to the correct form. Thus it is certain that the Elasmosaurs are not specialized for rapid progression through water.

Despite their small heads, all Elasmosaurs have a relatively very large gape, the quadrate being carried very far back. They have sharp pointed teeth which in the anterior part of the jaws (cf. *Microcleidus* and *Elasmosaurus*) are enlarged, directed forward, and interlocking. Such characters are always found in animals adapted for the capture of small quick-moving prey such as fish and cephalopods. The type-specimen of *Elasmosaurus platyurus* retained within the ribs remains belonging to the fish *Enchodus* and "*Sphyræna*" (? *Protosphyræna*); these forms are large, active and predaceous pelagic fish.

In addition to increase in length the neck of Elasmosaurids shows structural changes of great significance.

In *Microcleidus* and in all other Plesiosaurs of the same or earlier period, the cervical ribs are two-headed, rigidly attached to the centrum, and throughout the greater part of the neck quite long, directed backward and closely overlapping; they are in fact the characteristic " hatchet-shaped " ribs. These ribs owe their double heads and considerable length to inheritance from primitive forms. They show definite adaptations in the fact that they are attached solely to the centra, instead of articulating by their tubercles with processes from the neural arches, and in the closeness with which they overlap. These two features lead to increased rigidity of the long neck. The low attachment of the ribs, which with the neural spines divide the muscle masses of the neck into three equal sized parts, allows of a powerful development of obliqui colli and other similar muscles, and renders the intertransversari which pass between the ribs capable of depressing the neck and so opposing the muscles passing between the neural spines.

At the same time the closeness of the overlap between the ribs of the middle and late cervical region, which reduces the length of the intertransversari to about one centimetre, in an individual of *Microcleidus* five and a half metres in length, whilst increasing their breadth very considerably, renders the possible amount of lateral motion of the neck very small.

In all members of the Elasmosaur series the neural spines of the cervical vertebræ are rather high and very long, so that only very slight dorso-ventral flexion of the neck is possible. Thus the early Plesiosaurs have long and extremely stiff necks. They appear to have inherited this remarkable character from their ancestors, for *Nothosaurus* and other known Triassic forms have similar arrangements in the cervical region. This curious structure probably arose as an adaptation in these shore and shallow-water animals during their gradual acceptance of an aquatic life.

Between the stages represented by *Microcleidus* and *Murænosaurus* great changes take place in the cervical region. A single articular face replaces the two heads of the early type of cervical rib and probably represents the two fused; and the ribs, instead of being long rods overlapping for a considerable distance, are converted into short flattened processes projecting slightly downwards nearly at right-angles to the length of the centrum. The change from a two-headed to a single-headed rib has no very obvious significance, although it may allow of more powerful attachment and by decreasing the dorso-ventral thickness of the root of the process leave further space for muscles. The alteration in direction of the ribs lengthens the intercostal muscles, thereby increasing their range of action, decreasing the force they can exert at the same time. Thus the new arrangement allows of more extensive lateral movements of

the neck, sufficient strength being given by the powerful oblique muscles. There is no increase of the very slight dorso-ventral flexibility of the neck.

Thus we have seen that the later Elasmosaurs retain, and may even have increased their original powers of progression with a proportionately smaller muscle-mass, whilst they add to this the gradual development of an ability to turn rapidly by backing water with one paddle whilst going ahead with the other, and an enormous increase in length of neck together with a much enlarged capacity of lateral motion of the head. They have a mouth designed for the capture of small quick-moving prey. Finally, as shown by their world-wide distribution and occurrence in the Kansas and English Chalk, both laid down at a consider-able distance from land, they are clearly inhabitants of the open waters.

All the evidence is in fact consistent with the view that *Elasmosaurus*, surely one of the most remarkable of vertebrate types, is entirely and very perfectly adapted to a fish or cephalopod hunting existence on or very near to the surface of the open sea. Instead of securing prey by sheer speed the Elasmosaurids depend on the power of making very rapid lateral sweeps of the head of great amplitude, catching their food by sudden darts of the head whilst the body remains nearly stationary.

This mode of life and the series of adaptations on which it depends are not common to all later Plesiosaurs, and the changes considered in the foregoing discussion are hence not "advances" in the special sense in which I use that term. Nevertheless, like advances they develop steadily with time, each form showing a change from that before it in a direction which is the same whatever pair of stages be compared. Living as they did a pelagic life, the Elasmosaurids, from their first recognizable appearance in the Lower Lias to their disappearance in the Upper Cretaceous, must have had an environment which was very nearly unchanging—the temperature, meteorological conditions, composition of sea water, and in fact all their inorganic surroundings, can scarcely have differed at the beginning and end of their career, and as the whole ocean was open to them they could in all probability have avoided any change in conditions by changing their locality. As a matter of fact, the occurrence of *Elasmosaurus* in rocks of similar age in Kansas, England, and New Zealand suggests that, like the larger whales, they had a world-wide habitat and were to a large extent insensitive to physiographic changes over a considerable range.

The changes which went on in the fish and cephalopod faunas of the time considered can scarcely have been of much importance to the reptiles which fed on them, as every fish habit is represented in rocks of all the ages concerned: the Liassic Hypsicormids, for example, are as active and quick-moving as any fish which have lived since.

Thus we cannot in any way attribute the steady development of the unique Elasmosaur adaptations to change in environment or to the influence of migration. These animals, in fact, show the slow improvement of an animal mechanism along a definite line progressing toward a perfect fitness for a mode of life shared equally by the early and the late members of the series, under surroundings which retain a nearly complete uniformity.

It is interesting to contrast the history of the Elasmosaurids with that of a different line of Plesiosaurs, which, living side by side with them, from the first adopted a different diet, and show in consequence a different series of adaptations.

The series referred to is :—

" *Plesiosaurus rostratus* " ... Lower Lias. England.
Sthenarosaurus dawkinsi ... Upper Lias.   „
Peloneustes philarchus .... Oxfordian.   „
" *Dolichorhynchops osborni* ... Upper Cretaceous. U.S.A.

Animals of the type of *Dolichorhynchops* (*Polycotylus* ?) seem to appear in the English Chalk.

These animals are characterized by a short neck and a large head. The skull has a long contracted rostrum built up by the maxillæ and premaxillæ, and there is a long mandibular symphysis. The cervical vertebræ are never elongated, their ventral surface being divided into two by a median ridge which separates two depressed areas. Confirmatory evidence of the alliance of these forms can be found in the details of structure throughout, in the skull and limb-girdles.

This, the *Polycotylus* series, shows a gradual reduction in the length of the neck, the numbers of cervical vertebræ being :—

P. rostratus .... 27 ?
Sthenarosaurus .... 18 +
Peloneustes 22
Dolichorhynchops .... 19 ?

Not only is the number of elements in the cervical region reduced, but the individual vertebræ become shorter and shorter in proportion to their width. The head steadily increases in size. Thus in general form the Elasmosaur and *Polycotylus* series steadily diverge, the latter gradually acquiring something of the stream-line form of an ichthyosaur.

The large head and enormous gape of *Polycotylus* show that it fed on large animals, and its shape suggests that it captured them· by superior speed. It had thus not the same need for quick turning as *Elasmosaurus*, although requiring a higher rate of speed.

The series of figures of shoulder-girdles of Polycotylids, (text-fig. 12) shows only one steady change : the coracoid increases greatly in length, in area, and in the turning out of the postero-lateral corner. The humerus grows, if anything, longer

and its anterior border never becomes strongly concave. The dorsal ramus of the scapula (not shown in the figure of *Sthenarosaurus* because of its direct dorsal direction) does not

Text-figure 12.
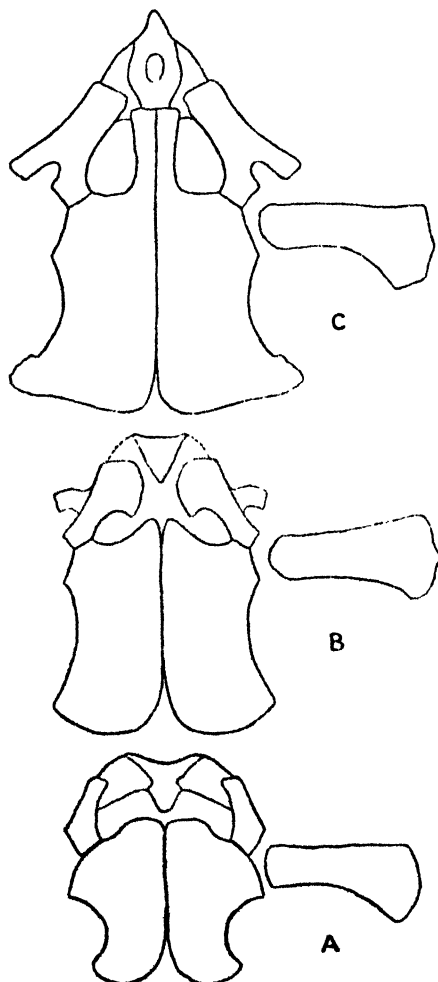
Shoulder-girdle and left humerus of a series of large-headed plesiosaurs.

A. *Sthenarosaurus dawkinsi* Watson.   B. *Peloneustes philarchus* Seeley.
C. *Trinacromeron osborni* Williston.

move forward and is not reduced, and the area of the preglenoid part of the girdle is not increased. The lack of great changes in the anterior part of the girdle shows that the power of

backing water, whose acquirement necessitated the great modification of this region seen in the Elasmosaurids, was not present in *Polycotylus*.

The elongation of the humerus is coupled with that of the coracoid, leading to the development of larger coraco-humeral muscles capable of a greater energy output, with a longer range of action and power of exerting a larger force. The longer humerus results in the retention of more distant muscle-insertions, reducing the rate of motion whilst increasing the power of the stroke of the arm. This change allows of the use of a paddle of larger area, with its centre of pressure further out. These changes are, however, not consistent with that reduction of the unflattened region of the exert part of the paddle and the more efficient type of insertion of muscles which are attained by the Elasmosaurids.

Thus the structure of the fore-limb and its girdle support the view suggested by its body form that *Polycotylus* was designed for rapid forward motion in the water.

The glenoid end of the scapula is relatively weak in *Polycotylus* because of their small power of backing water, the only action which produces forward thrusts of the head of the humerus on the anterior part of the glenoid cavity.

Only in one region are the changes of structure in the *Polycotylus* line similar to those amongst the Elasmosaurs. In *Polycotylus* the cervical ribs have become single-headed flattened processes exactly like those of *Muraenosaurus*, whilst in *Peloneustes* they resemble those of *Microcleidus*. This change results in an increased lateral flexibility in the short neck, an obviously desirable improvement.

Thus, starting from animals with somewhat similar structures, it is possible to trace in considerable detail the evolution of two entirely different types, and to provide a mechanical explanation of many of the changes in structure which occur, and correlate the whole with direct adaptation to divergent feeding habits.

It is actually possible to push the mechanical analysis into other regions of the body than those considered in this paper—the skull and lower jaw, the pelvis, hind limbs and tail, all showing similar series of changes directed toward adaptation to the characteristic modes of life.

The example of adaptation which forms the subject of this paper is of importance from its bearing on general evolutionary problems. It arises in a group of animals living under uniform conditions and not driven to the acceptance of that mode of life for which their adaptations especially fit them by any poverty of the environment. The direction of change in structure which occurs between any form and its immediate successor is the same whatever pair of forms be considered, and these changes are always in the direction of greater mechanical efficiency. The initial members of the two stocks considered are on the

whole very similar in structure, and there is no very obvious reason why their successors should have diverged so widely. It seems, however, that from the first they must have adopted different feeding habits in direct correlation with which their structure developed; that, in fact, in this case form followed on and was subservient to function.

The general lines of the scheme of evolution of the groups of Plesiosaurs which we have considered agree with the suggestions made many years ago by the late Prof. Williston, and substantiate by a more complete analysis of a much more abundant material the opinions his great experience led him to draw from the relatively incomplete specimens at his disposal.

The essential parts of the present work have long been known to me, and for many years I have looked forward to submitting them to the always kindly and invariably illuminating criticisms of Prof. Williston. His death has made this wish impossible of fulfilment, and I can only dedicate this essay, with all its imperfections, to the memory of a most distinguished palæontologist and a friend of charming personality.

EXHIBITIONS AND NOTICES.

May 6th, 1924.

Prof. E. W. MacBride, F.R.S., Vice-President,
in the Chair.

Dr. G. M. Vevers, F.Z.S., exhibited, and made remarks upon, a Leech (*Placobdella* sp.) from the American Terrapin *Chrysemys floridana*.

Mr. R. I. Pocock, F.R.S., F.Z.S., exhibited, and made remarks upon, a photograph of a Seal.

Prof. J. P. Hill, F.R.S., F.Z.S., exhibited, and made remarks upon, the Fœtus of a Fin-Whale.

Mr. D. Seth-Smith, F.Z.S., exhibited, and made remarks upon, two female Pheasants assuming male plumage.

May 20th, 1924.

Dr. A. Smith Woodward, F.R.S., Vice-President,
in the Chair.

The Secretary read the following Report on the Additions to the Society's Menagerie during the month of April:—

The registered additions to the Society's Menagerie during the month of April were 149 in number. Of these 91 were acquired by presentation, 16 were deposited, 29 were purchased, 1 was received in exchange, and 12 were born in the Menagerie.

The following may be specially mentioned :—

4 Persian Gazelles (*Gazella subgutturosa*) and 1 Griffon-Vulture (*Gyps fulvus*), from Mesopotamia, presented by Major W. C. F. Wilson on April 8th.

1 Seed-Snipe (*Thinocorys rumicivorus*), from the Falkland Islands, presented by P. Keith Cameron on April 24th.

1 Clouded Iguana (*Cyclura carinata*) from Goat Island, Jamaica, presented by Capt. A. M. Furber on April 27th.

2 Yellow-spotted Lizards (*Callopistes flavipunctatus*), new to the Collection, from the Desert of Tambey, North-West Peru, presented by Dr. Burgess Barnet on April 17th.

Major S. S. FLOWER, O.B.E., F.Z.S., exhibited, and made the following remarks upon, a remarkable Tortoise of the genus *Testudo* :—

This individual is of interest in two ways :—

Exact age is known.

It was hatched in the Giza Zoological Gardens on the 3rd Sept., 1916. The approximate size of the carapace of one of these tortoises when newly hatched is in length and width about equal, *i. e.* 33 millimetres. As the tortoise grows the length soon exceeds the width. At about two months old the length would be 44, the width 36 mm. Most of the growing of these tortoises appears to take place within their first three years, when the carapace attains to a length, in the median line in a straight line, of 100 to 130 mm. Later the rate of growth becomes slower and more irregular.

Length :—

Four 6-year old individuals varied from 154 to 165 mm.

Five 7-year „   „   „   „   166 „ 192 „

Two 10-year „   „   were respectively 137 and 161 mm.

The individual exhibited is 156 mm. in length and 112 mm. in width of carapace ; it has not increased in size during the last year and a half.

Appearance.

31 of these tortoises have been hatched in the Giza Zoological Gardens in the years 1907 to 1923. The country of origin of their parents is not known, unfortunately.

The marked depression of the carapace and the domed shape of the vertebral, and of the fourth costal shields, may be merely the result of being bred under the artificial conditions of captivity.

In the standard work on Tortoises, Mr. G. A. Boulenger's 'Catalogue of Chelonians,' British Museum, 1889, on pages 154 and 155, a key is given for distinguishing the land tortoises of the Palæarctic fauna.

There can be no doubt that these tortoises bred at Giza belong to the species which Mr. Boulenger calls *Testudo ibera* (*op. cit.* p. 176), but the individual now exhibited would not find its place by the key on two points :—

(i.) The Asiatic *T. horsfieldi* differs from the four species which occur in the Mediterranean area—*T. marginata, leithii, ibera,* and *græca*—by having only four claws on the hand instead of five, as in those four species.

Of the 31 hatched at Giza, 12 had four claws, 7 had 5 (in these cases the 5th claws appeared smaller than normal), and in 12 cases this character was not noted.

All other specimens of these four species that I have had opportunities of examining (with one possible exception in a *Testudo leithii*) had five claws on the hand.

(ii.) Character of comparative breadth of the third and fifth vertebral shield has been used to distinguish species in this group, *Testudo marginata. leithii*, and *ibera* having the fifth shield not broader than the third, while *T. græca* has the " fifth vertebral much broader than third."

In these Giza bred tortoises this character appears to alter with age, in five of the youngest individuals examined the third vertebral was wider or about equal to the fifth, in eleven older individuals (including the one now exhibited) the fifth vertebral is broader than the third.

Mr. F. MARTIN DUNCAN, F.Z.S., exhibited, and made remarks upon, the skin and hair of a Platypus (*Ornithorhynchus anatinus*) from Tasmania.

Miss E. M. KNOBEL, F.Z.S., exhibited, and made remarks upon, the pelvic bones of the Blue-fronted Amazon and other Parrots.

Sir SIDNEY F. HARMER, K.B.E., Sc.D., V.P.R.S., F.Z.S., exhibited a piece of ambergris which had been presented to the British Museum (Natural History) by Mr. C. F. Herlofson, of the Compañia Ballenera Española, Algeciras. During a visit to Algeciras in April of this year, he had had the opportunity of seeing a series of ovoid masses of this substance, which had recently been removed from the rectum of an old male Sperm Whale captured by the Spanish Company in the Straits of Gibraltar; and the portion exhibited (with a photograph of these masses in the fresh condition) was a portion of one of them. The pieces when inspected were still moist, and had only partially lost their fæcal odour. Some of them showed included Cephalopod beaks, a feature which is characteristic of genuine ambergris. The specimen is of considerable interest, in view of the fact that its origin is definitely known.

June 3rd, 1924.

Prof. E. W. MACBRIDE, F.R.S., Vice-President,
in the Chair.

Mr. D. SETH-SMITH, F.Z.S., exhibited, and made remarks upon, a photograph of Elephant twins.

ON THE FORE-BRAIN OF SPHENODON PUNCTATUS.

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Brain Roof.

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ON THE FORE-BRAIN OF SPHENODON PUNCTATUS.

ON THE FORE-BRAIN OF SPHENODON PUNCTATUS.

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ON THE FORE-BRAIN OF SPHENODON PUNCTATUS.

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ON THE FORE-BRAIN OF SPHENODON PUNCTATUS.

ON THE FORE-BRAIN OF SPHENODON PUNCTATUS.

ON THE FORE-BRAIN OF SPHENODON PUNCTATUS.

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ON THE FORE-BRAIN OF SPHENODON PUNCTATUS.

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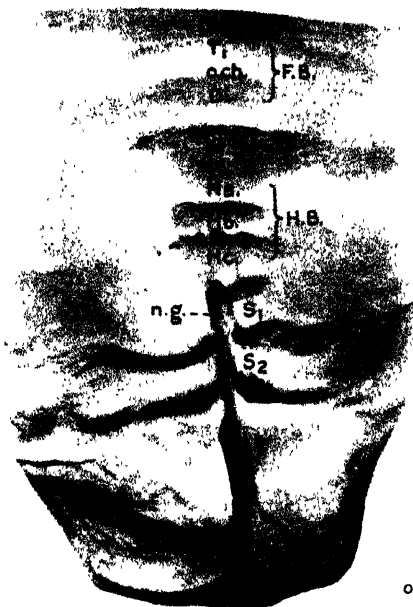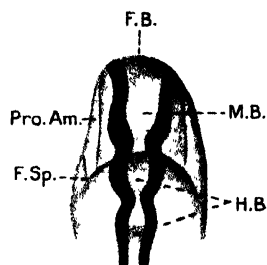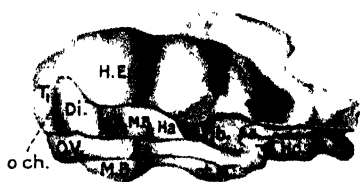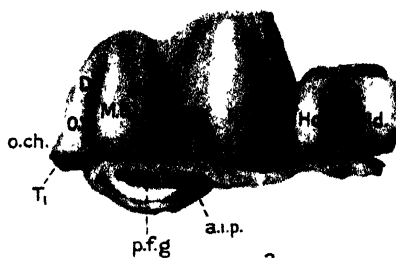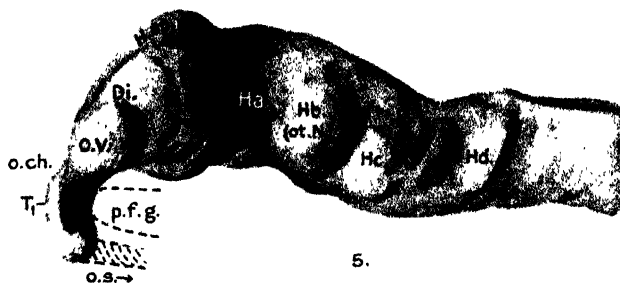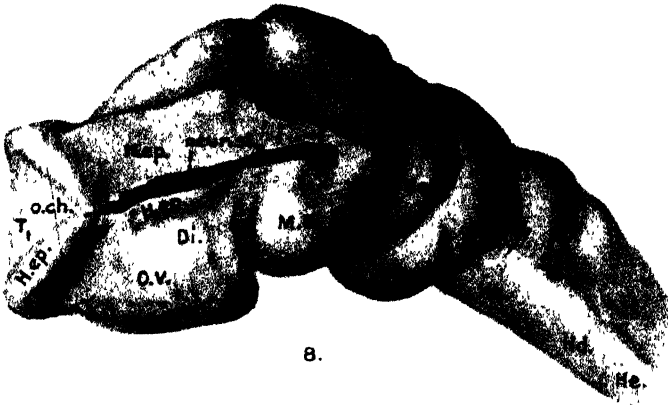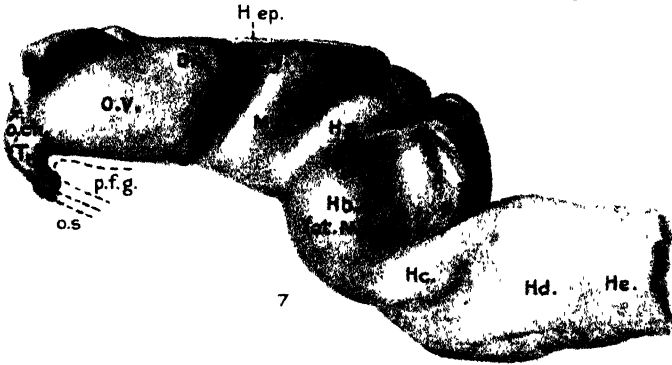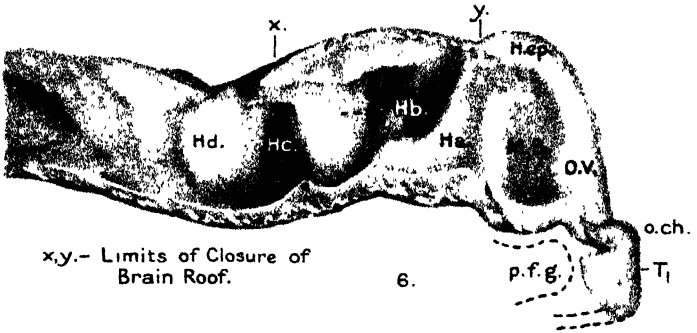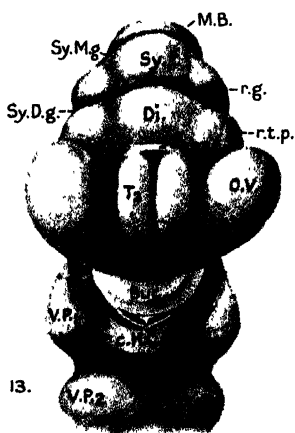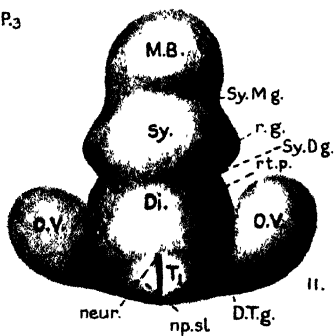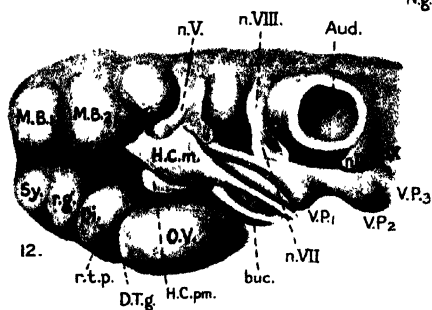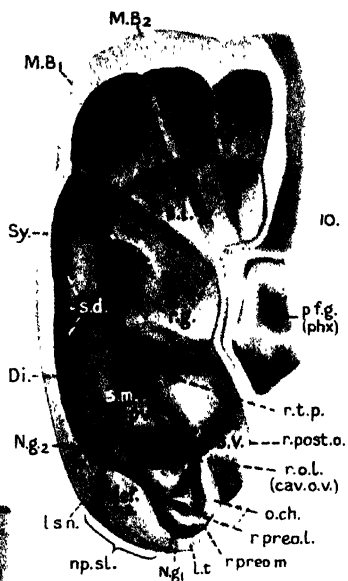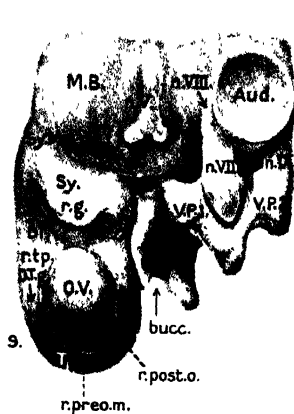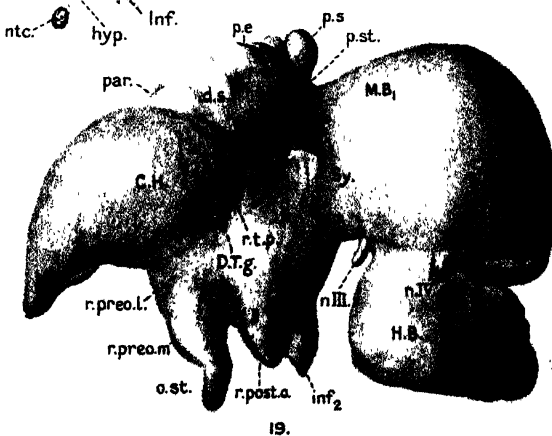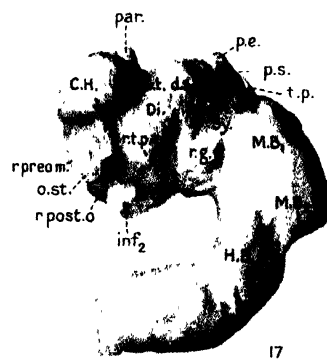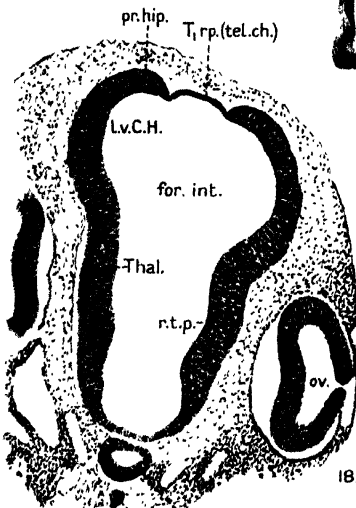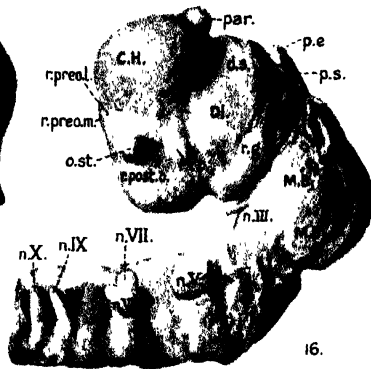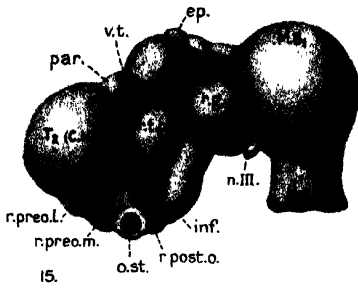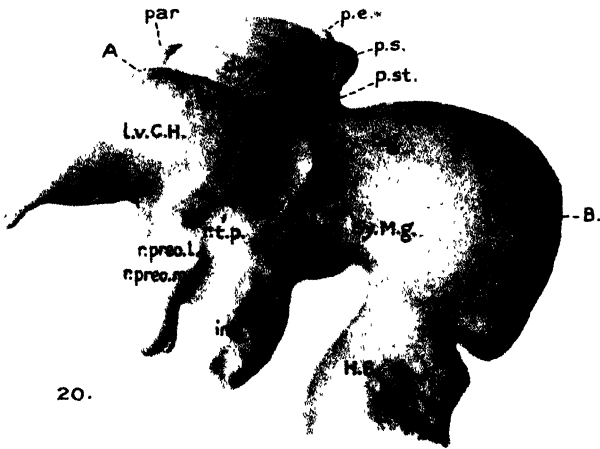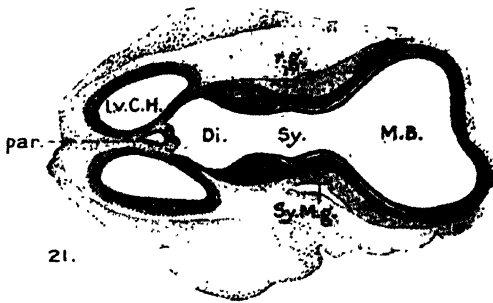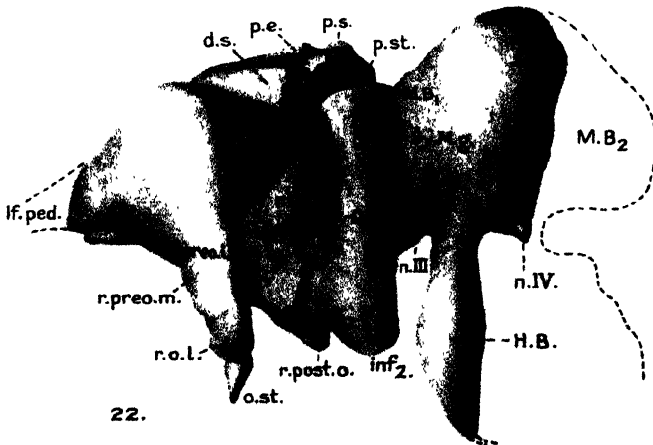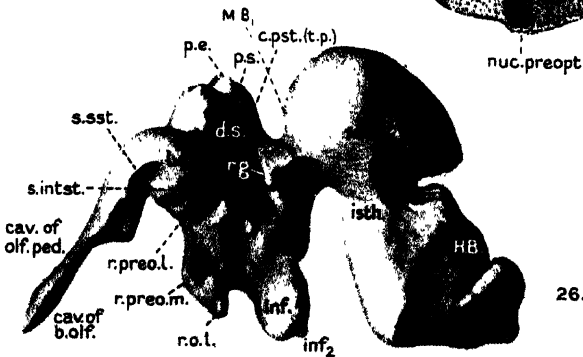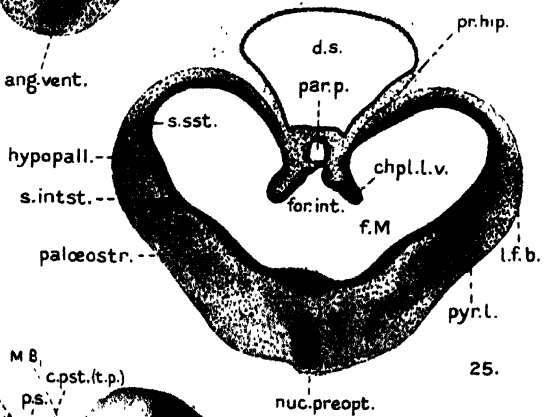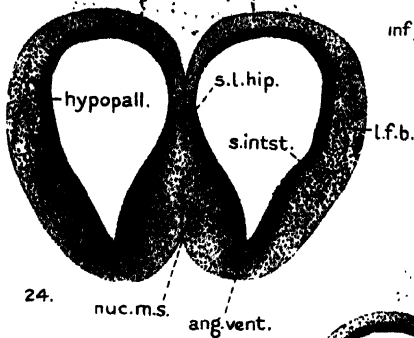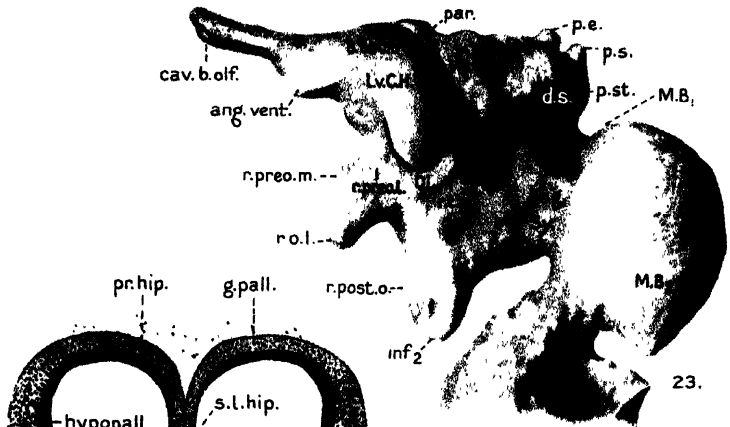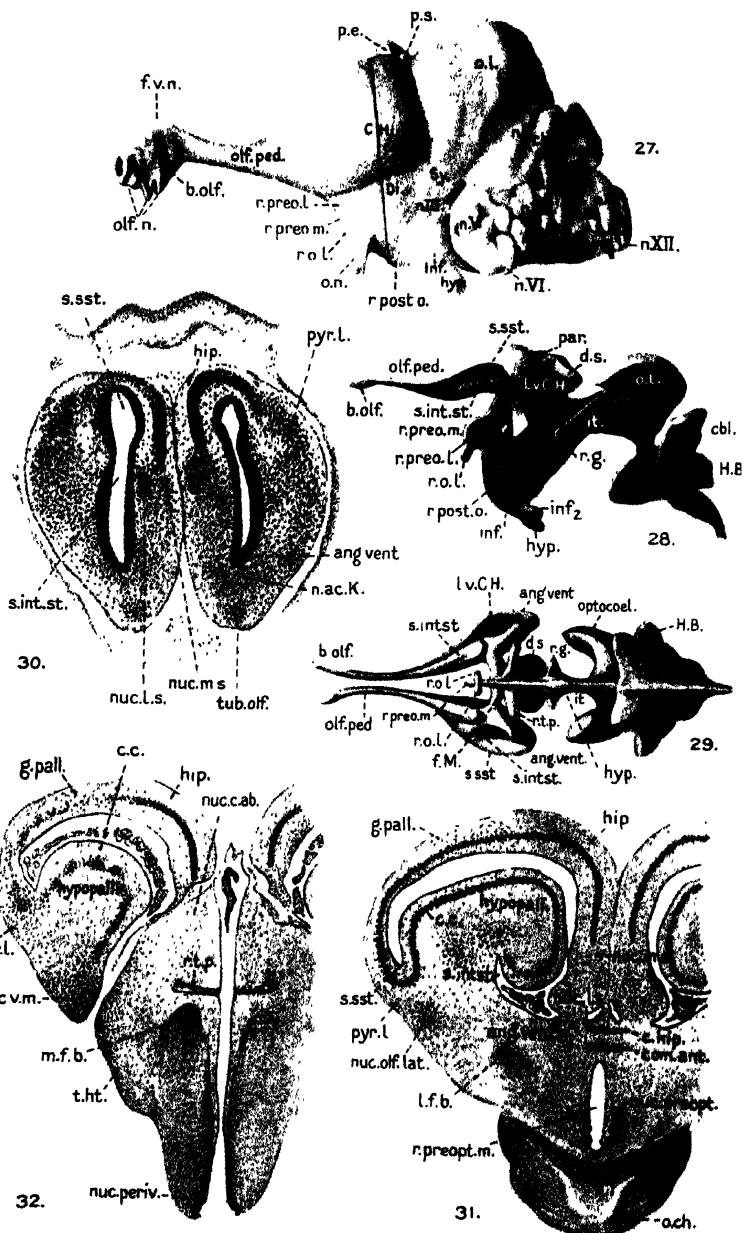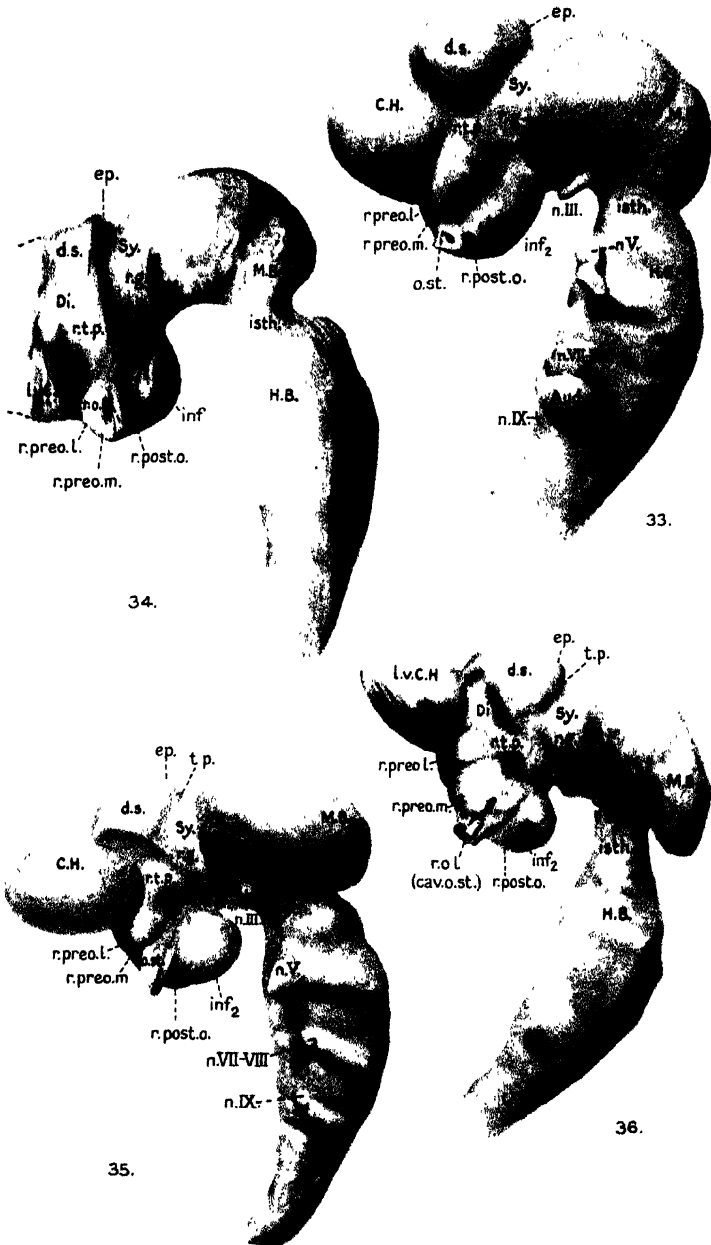
ON THE FORE-BRAIN OF SPHENODON PUNCTATUS.
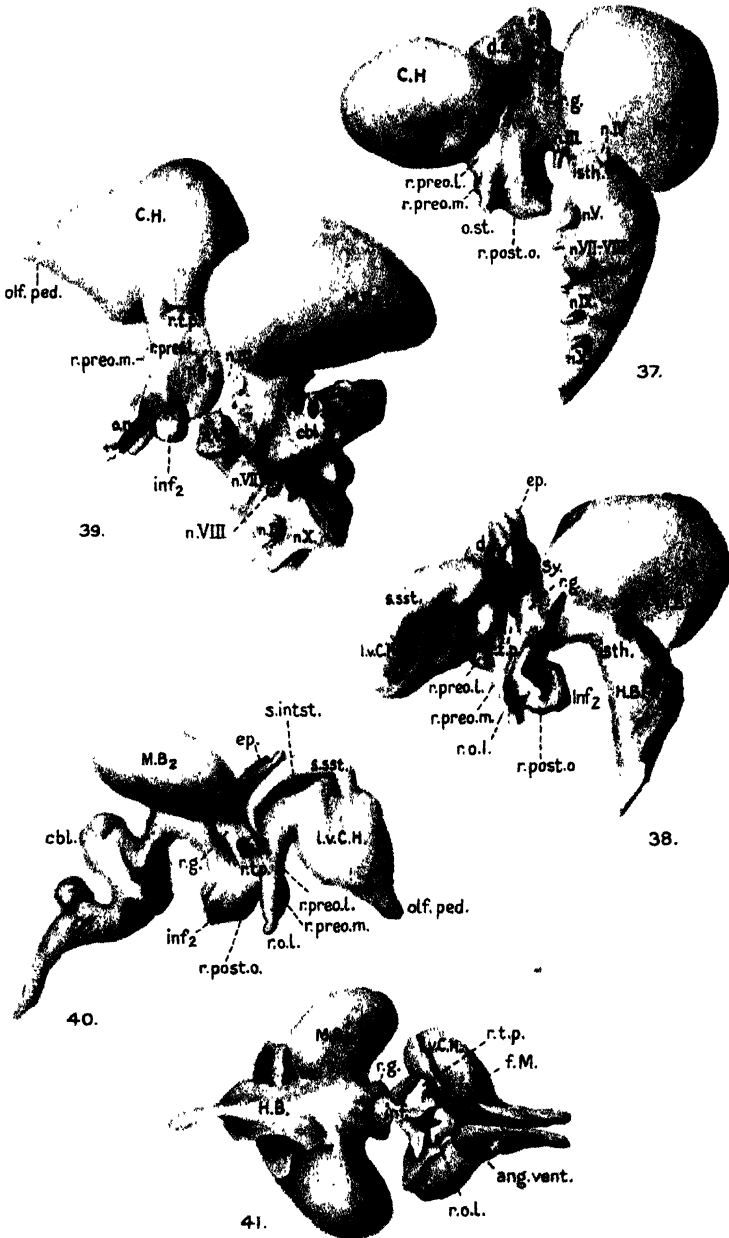
40. The Development and Neuromery of the Fore-Brain in *Sphenodon punctatus*, with special reference to the presence and neuromeric significance of certain paired metameric diverticula of the central cavity of the Fore-Brain. By the Rev. FRANK JOHN WYETH, D.Sc., M.A., B.D., F.Z.S. (sometime Exhibitioner of St. John's College, Cambridge).

[Received June 3, 1924. Read October 21 1924

(Plates I. IX.)

CONTENTS.

1. INTRODUCTION.

The present paper is an attempt to elucidate the chief features of the development of the fore-brain of *Sphenodon*, with special reference to certain paired metameric diverticula of the central cavity of the brain which occur therein, and their possible bearing upon the neuromeric analysis of the brain. The neuromery of the mid-brain and hind-brain will be considered in a second paper.

The presence " in addition to the ventricles of the cerebral hemispheres and pineal outgrowths and optic lobes, of three pairs of lateral diverticula of the central cavity of the brain of *Sphenodon*," was noted by Professor Dendy in 1910. He gave a brief description of them in embryos of Stages R and S, and in adult *Sphenodon*, and suggested that they may have an important bearing on the neuromeric analysis of the brain. To the most anterior pair of these diverticula he gave the name of recessus optici laterales, on the assumption that they were the persistent vestiges of the cavities of the primary optic vesicles. This assumption has now been found to be correct, and the name has therefore been retained in the present paper. These recesses have been figured as parts of the recessus preopticus in, among others, the following animals: *Gadus morrhua* (Kappers, 1906), *Rana mugiens* (Kappers, 1918), *Varanus salvator* (De Lange, 1911), *Monopterus javanensis* (Van der Horst, 1917); while

Gisi (1907) in her paper on *Sphenodon*, (fig. G), indicates the recess and marks it "Ausstulpung d. ventrikels." It would appear that the presence of this pair of recesses has been observed, the assumption made that they represent,—as they undoubtedly do,—the persistent vestiges of the cavities of the primary optic vesicles, and that no further attention has been paid to them : their possible value as evidence of the serial homology of diverticula of the central cavity of the brain being ignored.

The second pair of diverticula, which Dendy calls the recessus thalami prænucleares, appear to have escaped identification, although Gisi (*op. cit.* p. 47) describes a small oval recess lying in a groove between the nucleus thalami anterioris and the nucleus rotundus, and Rendahl (1924, figs. 39, 40) shows a similar recess in the brain of a chick embryo, and calls it "Segmenthöhle das Parencephalon." In each case the recess indicated is probably one member of the paired recessus thalami prænucleares.

The third pair of recesses Dendy names recessus geniculorum, and it is shown below that they are apparently homologous with the identically-named recesses of the Mammalian fore-brain, although Dendy (1910, p. 249, footnote) appears inclined to assign them to the first neuromere of the mid-brain. One of these recesses is shown by Gisi (fig. G), and Rendahl (fig. 40) indicates, but does not name, a similar recess in the synencephalon of a chick embryo.

Of the other diverticula now under consideration, in view of their discussion in a later section of this paper, it seems necessary only here to note that the serial homology existing between the cerebral hemispheres and the primary optic vesicles is now generally admitted, that Dendy (1910, pp. 308–314, and pp. 329–331) has carefully reviewed the evidence of the bilateral origin of the pineal organs of Cyclostomes, Fishes, Amphibians, Reptiles, and Birds, and that it now appears quite legitimate to regard the pineal organs as dislocated members of a pair of structures serially homologous with the lateral eyes.

2. MATERIAL AND METHODS.

Professor Dendy again most kindly placed at my disposal the whole of his unrivalled collection of sections of embryo and adult specimens of *Sphenodon*, a detailed list of which was given in an earlier paper (Wyeth, 1924, p. 4), and the methods of examination adopted were those described in the same section of that paper, models of the brain, and in most cases of its cavities also, being made in order to illustrate the principal stages of development.

For comparative purposes sections were examined, and in some cases models were prepared, of the brain of embryos of *Scyllium*, *Acanthias*, *Gecko*, *Columba*, and the Chick.

For the sake of brevity there has been given in the descriptive sections which follow, a detailed account of only those embryos

illustrating the more important developmental features, and in the case of others reference only is made to those structures that are essential to the present purpose. It is presumed that the other chief features of development and general morphology are sufficiently indicated in the figures accompanying this paper.

3. TERMINOLOGY.

Such an extensive nomenclature has been used, and so differently applied by different authors that it seems desirable to state some of the more important terms and definitions which have been adopted in this paper. They are, in general, those proposed by Herrick (1910, pp. 492 ff., and 1921, p. 432).

The terms rostral and caudal, dorsal and ventral, are to be interpreted morphologically and not merely topographically, *i. e.* they are to be considered in reference to the morphological axes of the neural tube, and in using them any topographical changes due to temporary and variable modifications, such as *e. g.* cranial flexure, are ignored.

The *telencephalon* is regarded as the terminal segment of the primitive neural tube together with its secondary derivatives, including the paraphysis, the velum transversum, and those paired dorso-lateral evaginations to which during the later stages of development the name cerebral hemispheres is applied.

The unevaginated portion of the primitive end-brain is called the *telencephalon medium*, the persistent portion of its ventricle included between the optic chiasma and the lamina terminalis being referred to as the *recessus preopticus medius*. The ditelencephalic boundary is that proposed by Johnston (1909), and now generally accepted, viz., dorsally the caudal surface of the velum transversum, ventrally the caudal border of the chiasma ridge, and laterally a line passing along the wall of the fore-brain and connecting the lateral extremities of these two structures.

The rostral segment of the between-brain is called the *diencephalon* (anterior diencephalic segment or parencephalon, auctt.), and is found to be a single neuromere, as is also the caudal segment or *synencephalon*.

The mid-brain is of course termed the *mesencephalon*, and reasons will be adduced for considering it to be composed of a rostral and a caudal neuromere.

For that dorsal extension of the ingrown pallium which lies between the pallial roof and the palæostriatum and occupies a great part of the lateral ventricle of the cerebral hemisphere I have adopted the term *hypopallium* invented by Elliot Smith (1919). He has shown that it is cortical in origin, and not striatal as implied by De Lange and Kappers. Johnston (1915) calls it the dorsal ventricular ridge, and De Lange (1913) calls its anterior part neostriatum and its posterior part epistriatum, the last of which terms Edinger (1896), as Elliot Smith points

out, had already used in four different and conflicting senses. Since writing the above I notice that Miss Hines (1923) calls this structure the neostriatum, but I still think that Elliot Smith's term hypopallium is to be preferred, as it emphasises the pallial nature of the structure and also avoids the ambiguity and erroneous implications consequent upon the adoption of any of the other terms enumerated above.

4. GENERAL MORPHOLOGY OF THE FORE-BRAIN, WITH SPECIAL REFERENCE TO THE DIVERTICULA OF ITS CENTRAL CAVITY.

Each embryo is identified by its number in Prof. Dendy's collection, and the stage of development it has attained is denoted by a letter. The system of lettering is that first proposed by Dendy (1899), and now generally adopted by British zoologists. Histological details are given only when they appear to be germane to the subject now under consideration.

For the purpose of comparison a number of figures of the fore-brain and its cavity in certain Chick embryos have been included in this section. A detailed description of the development of the fore-brain of the Chick is outside the scope of the present paper, and has recently been given by Rendahl (1924), with whose observations my own are in essential agreement. The only developmental feature respecting which I desire to record a conclusion differing from that expressed in his paper is discussed in Section 6 below.

Stage D.

Embryo No. 58 was examined and modelled (Pl. I. fig. 1). This is the youngest embryo in which the neural groove shows any trace of differentiation into head and trunk regions, and it is notably similar in general configuration to the 2-somite human embryo (No. 1878 of the Carnegie Collection), described by Ingalls (1920), and figured by Bartlemez (1923, fig. 1).

The dorsal surface of the medullary plate of this embryo exhibits near its anterior extremity a transverse crescentic furrow, the convex curvature of which is anteriorly directed. This is the rudiment of the oral sinus, and its central portion is bounded caudally by a low transverse ridge, the anlage of the optic chiasma ridge, the anterior surface of which constitutes the rudiment of the floor of the rostral portion of the fore-brain, the primary telencephalon. Immediately caudad of the ridge is an ill-defined shallow transversely elongated oval depression, which represents the caudal portion of the fore-brain, and ultimately gives rise to the diencephalon and the synencephalon. Caudad of this the neural groove widens and deepens somewhat abruptly to form the mesencephalic dilatation, the axis of the neural groove simultaneously bending somewhat sharply in a ventral direction, producing the cranial flexure, which aids in identifying this region as mid-brain.

Immediately caudad of this the groove becomes somewhat narrower and presents a series of three well-marked dilatations, the second of these being considerably the largest. These are the rudiments of the three primary segments of the hind-brain. It is proposed to show in a subsequent paper that these three segments give rise to the seven definitive neuromeres of the hind-brain.

It may perhaps be desirable somewhat to anticipate by stating that from the most rostral of these segments are derived the first, second, and third of the hind-brain neuromeres, from the caudal segment arise the fifth, sixth, and seventh of these neuromeres, while the conspicuous middle segment is found to be the fourth hind-brain neuromere (otic neuromere), as already demonstrated in human embryos by Bartlemez (1922 and 1923).

As he points out, the presence of this definitive neuromere during so early a stage of development (human embryo of two somites, and in *Sphenodon* Stage D) seems to indicate that the primitive segments now observed and the definitive neuromeres are expressions of the same fundamental metamerism, and he also observes that Smith (1912) has expressed the same idea in his statement that in *Cryptobranchus* certain inter-neuromeric grooves have a marked tendency to appear earlier than others.

In the present paper the divisions of the hind-brain will be called "segments," thus avoiding any premature implications respecting their individual relationship to definitive neuromeres.

Caudad of the hind-brain region the neural groove becomes much narrower and somewhat more shallow. It exhibits rudiments of two pairs of somites, each pair being separated from the hind-brain and from one another by conspicuous transverse grooves (intersomitic grooves).

Stage E.

Embryos Nos. 56 and 64 were examined, and the latter was modelled (Pl. I. figs. 2, 3, 4).

In these embryos the neural groove is still widely open, but in the mid-brain and hind-brain regions the neural folds have conspicuously expanded dorsally, and have begun to incurve preparatory to undergoing fusion along the mid-dorsal line to complete the roof of the brain.

In the fore-brain region the folds are much less developed, and the neural groove is much shallower and more widely open. The chiasma ridge is becoming conspicuous, and the floor of the fore-brain immediately rostrad of it (the rudiment of the primary telencephalon) is short and ventrally flexed, and terminates rostrally in a well-marked lip, anterior and ventral to which is the deep oral sinus. Caudad of the chiasma ridge the cavity of the posterior part of the fore-brain considerably widens and deepens, and its floor is bounded caudally by a well-marked transverse internal ridge, which with a corresponding external

furrow indicates the boundary between the fore-brain and the
mid-brain. The lateral walls of the fore-brain rise abruptly,
causing it to assume the form of a deep cup widely open dorso-
rostrally. It is, however, considerably smaller than the mid-
brain segment. Each of the lateral walls of the fore-brain bears
externally a conspicuous oval dorso-lateral thickening merging
antero-dorsally with the head-epiblast. This thickening is the
primordium opticum (rudiment of the primitive optic vesicle),
which has already been described in early human embryos by
Bartlemez (1922). In *Sphenodon* it becomes conspicuous some-
what earlier than does the primordium oticum.

The mid-brain is a large rounded vesicle, and caudad of this
the hind-brain now exhibits four dilatations, the second of these
still being the most conspicuous. Dorso-laterally of this hind-
brain segment the head-epiblast shows two somewhat ill-defined
thickened areas, similar to those described in human embryos by
Wilson (1914) and Bartlemez (1922)—the primordia otica.

A more detailed description of this embryo is not now given,
as it is considered that its essential features are sufficiently
indicated for the present purpose in Pl. I. figs. 2 and 3.

It seems desirable to note that Bartlemez (1923, pp. 240-241
and fig. 5) points out that in describing the early embryos of
certain other Vertebrates some earlier observers appear wrongly
to have identified the mid-brain as part of the fore-brain, and to
have interpreted the convex lateral walls of the mid-brain as the
rudiments of the primitive optic vesicles. It would appear that
these writers have overlooked the existence of the short rostral
portion of the fore-brain and that they have regarded the
primordia optica as merely a thickened lip of the amniotic fold.
On the other hand, it must be noted that Dendy (1899—fig. 21,
now reproduced as fig. 4) agrees with the present interpretation
of the embryo now under consideration; and a careful com-
parison of this embryo with those of the immediately subsequent
stages of development,—with particular reference to the relative
positions of the primitive fore-gut, the cranial flexure, the
primordia optica and otica, and with the subsequent development
of the brain segments,—appears conclusively to prove the
correctness of the present interpretation, which agrees with,
among others, those of Giglio-Tos (1902), Low (1908), Ingalls
(1920), and Bartlemez (1922 and 1923).

Stage F.

Embryos Nos. 61 and 72 were examined, and the former was
modelled (Pl. I. fig. 5 and Pl. II. fig. 6).

The fore-brain is more conspicuous than it was in the
preceding embryo, and forms a short, wide, oval vesicle, widely
open dorsally, its cavity being continuous with that of the
amnion. The chiasma ridge clearly divides the fore-brain into a
rostral region, which will in future be called the *telencephalon*,

and a larger caudal portion, the *diencephalon*, in the caudal portion of which the *synencephalon* soon becomes differentiated. The lateral walls of the diencephalic region are well-developed and incurved dorsally, and although they converge caudally they do not yet meet in the mid-dorsal line, the whole of the fore-brain still being roofless.

The conspicuous primitive optic vesicle of each side now occupies nearly the whole of the latero-dorsal wall of the diencephalon, and an internal ridge and corresponding external furrow indicating the boundary between the fore-brain and the mid-brain are very conspicuous.

The mid-brain or *mesencephalon* is a large oval transversely elongated vesicle, a strong constriction dividing it from the hind-brain. Its strongly convex lateral walls fail to meet in the mid-dorsal line, although they closely approach one another caudally, and throughout the hind-brain region the roof formation is complete.

The hind-brain or *rhombencephalon* is approximately pyriform, its cross-section being considerably less than that of the mid-brain, and tapering caudally. Five hind-brain segments can now be distinguished. The rostral of these is a somewhat narrow and short cylindrical segment, the second, or otic, constitutes the large swollen central hind-brain region, while caudad of this the original third or caudal segment exhibits a series of three small dilatations which are ultimately found to be the three caudad definitive neuromeres of the hind-brain.

The rostral part of the head of this embryo is slightly tilted backwards and upwards, two flexures of the cranial axis thereby being produced. The more rostral of these is that commonly found in the mid-brain region of many Vertebrate embryos, while the more caudal flexure, which involves the middle and caudal parts of the hind-brain, is a purely temporary phenomenon occurring only during this and the immediately subsequent stage of development.

Stage G.

Embryo No. 59 was examined and modelled (Pl. II. figs. 7 & 8). In this embryo the external differentiation of the brain-segments is much more distinct than during the preceding stage of development; the primitive optic vesicles are much larger and more conspicuous, and rostral of the first hind-brain segment the head is sharply bent to the left. This lateral displacement of the rostral part of the head occurs also in an embryo of Stage H (No. 78).

The dorsal closure of the neural groove has considerably progressed, the borders of the lateral walls of the diencephalon being separated in the mid-dorsal line by only the narrow neuroporic slit, while caudad of the extreme rostral region of the mesencephalon the brain-roof is complete.

The *telencephalon* is still comparatively short and somewhat ventrally flexed. Its lateral walls are now well developed, but are still widely separated antero-dorsally.

The *diencephalon* has enormously increased in size, and the large primitive optic vesicles have assumed the ovoid shape which is characteristic of their later stages of development, and they occupy nearly the whole of the lateio-dorsal walls of the diencephalon, their position during these early stages of development conclusively proving them to be dorsal derivatives of this brain-segment.

The *synencephalon*, which first becomes conspicuous during Stage J, is now distinguishable, its floor being defined by, and included between, a low transverse internal ridge crossing the caudal region of the floor of the fore-brain, and the ridge which constitutes the boundary between the fore-brain and the mid-brain.

The diencephalon and rudimentary synencephalon together are now wider than, and nearly twice as long as, the *mesencephalon*, the fore-brain therefore becoming the most conspicuous of the three brain components.

The *rhombencephalon* differs but little from that of the preceding embryo, its changed contour being due to the accentuation of the temporary cranial flexure which occurs in this region.

Stage H.

The only available embryo (No. 78) of this stage of development, which had been mounted whole, was examined.

The chief developmental change to be detected therein is the further increase in size of the primary optic vesicles, each of which is now a large and nearly hemispherical evagination.

In the hind-brain region the auditory epiblastic patches, or rudimentary auditory pits, appear as a pair of clearly defined shallow oval depressions of the head epiblast, their position confirming the foregoing identification of the otic neuromere.

Stage J.

Two embryos of this stage were examined and modelled.

The younger, early Stage J, No. 44, is shown in Pl. III. figs. 9, 10, and 11, and the older, late Stage J, No. 79, in Pl. III. figs. 12 and 13.

In embryo No. 44 the angle of cranial flexure is rather greater than 90°, the morphologically rostral extremity of the brain therefore becoming topographically ventral. The fore-brain and mid-brain together constitute a large pyriform structure, its longer axis being rostro-caudally directed, while its slightly smaller caudal region occupies the topographically dorsal apex of the angle of cranial flexure (Pl. III. fig. 9).

Telencephalon.

The antero-dorsal extremity of the neural tube is still open, the conspicuous slit-like neuropore extending dorsally from the ventral apex of the telencephalon to bisect the anterior quarter of the roof of the fore-brain. The ventral extremity of the neuropore defines the position of the morphologically rostral end of the neural tube, and the terms "rostral" and "caudal," "dorsal" and "ventral" can now be used relative to this and applied without qualification. Closure of the *neuropore* appears to be proceeding by the fusion of a conspicuous infold of the right border of the telencephalic roof which projects into the brain-cavity, with the free border of the roof to the left of the slit. Caudally the neuropore dilates, the terminal circular aperture thus produced probably being the region of final closure or definitive neuropore, the general appearance of the structures concerned suggesting that the process takes place in the rostro-caudal direction. The point of final closure marks the position occupied by the *recessus neuroporicus internus* after the closure has occurred, and indicates the junction of the caudal extremity of the lamina terminalis with the rostral border of the lamina neuroporica.

As the position and morphological value of these structures have been differently interpreted by various authors (Johnston, 1911, pp. 491–493), it may be well to re-state the definitions now generally accepted. The *lamina terminalis* is the region of closure between the recessus neuroporicus and the chiasma ridge, and in it converge and meet the floor-plate and the roof-plate of the telencephalon. The *lamina supra-neuroporica* is the region of closure from the recessus neuroporicus to the velum trans-versum (Johnston, 1911, *op. cit.*). Caudad of the neuroporic slit the ventral surface of the fore-brain exhibits a conspicuous primitive infundibulum, while the internal angle of flexure is occupied by the much smaller floor of the mid-brain.

The wide shallow *di-telencephalic groove* appears just laterad of the mid-dorsal point of the roof of the fore-brain, passes latero-ventrally until it reaches a point on the brain-wall just dorsal to the primitive optic vesicle, and runs rostrally to disappear slightly laterad and ventrad of the neuropore. Immediately rostrad of this groove a short transverse ridge, so low as to be hardly visible, crosses the roof of the fore-brain. This ridge is the rudiment of the paraphysial evagination, and the inconspicuous groove which bounds it caudally is the anlage of the *velum transversum*. A low ridge corresponding to the di-telencephalic groove is visible on the inner surface of the wall of the fore-brain, and included between it and the rostro-dorsal roof is the wide cavity of the primary telencephalon (*telencephalon medium*). The deep dorsi-ventrally directed central portion of this cavity is homologous with the sulcus limitans hippocampi of Selachians and Amphibians, and it exhibits a central oval pocket which is evidently a

lateral diverticulum of the telencephalic cavity homologous with Deudy's other lateral diverticula, viz. the recessus thalami præ-nuclearis and the recessus geniculi. This pocket I have called the *recessus preopticus lateralis.* The prominent chiasma ridge forms the · caudo-ventral boundary of the telencephalon, and between it and the dorsal border of the neuropore the rostral wall of the brain consists of the thick lamina terminalis, dorsal to which the still thicker lamina supra-neuroporica forms the roof of the telencephalon. A low transverse ridge, which indicates the site of the future *commissura anterior,* crosses the middle region of the lamina terminalis, and immediately rostrad of this ridge is a small *recessus ventricularis,*— a typically reptilian feature. The *recessus preopticus medius* is well defined.

Diencephalon.

The thin roof of the diencephalon forms a low dome occupying the middle third of the roof of the fore-brain and is bounded caudally by the di-synencephalic groove, which is very shallow dorsally, deepens and widens latero-ventrally and disappears in the furrow which separates the primitive infundibulum from the post-tubercular recess. The primitive optic vesicles are large, ovoid, and dorso-ventrally elongated, occupying the greater part of the rostral third of the lateral surface of the fore-brain. Between the di-synencephalic groove and the primitive optic vesicle the lateral wall of the diencephalon bears a fairly promi-nent dorso-ventral ridge corresponding to which is a deep diverticulum of the neuromeric cavity (Johnston's primary optic furrow), from the antero-dorsal part of which the primitive optic vesicles are developed, and the persistent postero-lateral vestige of which is the recessus thalami prænuclearis. On the floor of the fore-brain the tuberculum posterius— a short transverse ridge caudad of the primitive infundibulum—forms the caudal boundary of the diencephalon. The cavity of the primitive optic vesicle communicates with that of the diencephalon by a large oval aperture.

The condition now obtaining not only confirms the previous suggestion that the *primitive optic vesicles originate as a pair of dorso-lateral evaginations of the rostral part of the wall of the diencephalon,* but also indicates that *the recessus thalami præ-nucleares are paired lateral diverticula of the cavity of the same neuromere.*

The *Synencephalon* is now well developed. Its roof is a low dome clearly visible in only the mid-dorsal region, but the medio-lateral wall bears a very conspicuous conical prominence, somewhat elongated dorso-ventrally, which is the external expression of the deep conical diverticulum of its cavity which persists as the recessus geniculi. The fairly conspicuous floor of this neuromere is occupied by the post-tubercular recess, which is included between the tuberculum posterius and the small ridge which marks the highest part of the habenular flexure (Kingsbury, 1922).

In late Stage J (Embryo No. 79, Pl. III. fig. 13) the neuropore is closed, its position being indicated by the small recessus neuroporicus internus. The secondary telencephalic evaginations have appeared as a pair of rostro-caudally elongated low oval eminences, the rudiments of the cerebral hemispheres, separated in the mid-dorsal line by a conspicuous groove, the caudal part of each having undergone the greater development. This is similar to the condition observed in Amphibian embryos, and is probably a primitive feature. The recessus preoptici laterales are larger than they were in the younger embryo of Stage J, as are also the paraphysial arch and the velum transversum. The constricting-off of the primitive optic vesicles from the diencephalon has considerably progressed, especially ventrally, the stalk region being much more clearly defined. The roof of the synencephalon is more convex, and this neuromere is more clearly differentiated than it was in the preceding embryo.

The Sulci of the Fore-Brain.   (Pl. III. fig. 10.)

On the lateral wall of the fore-brain of embryos of this stage of development typical and conspicuous sulci can be distinguished.

The *sulcus limitans* passes rostrally across the middle level of the lateral wall of the mesencephalon, traverses those of the synencephalon and diencephalon and then curves rostro-ventrally across the wall of the telencephalon to terminate on the lateral wall of the recessus preopticus medius.

It will later be observed that the recessus preopticus lateralis, the recessus thalami prænuclearis, and the recessus geniculi are situated along the course of this sulcus, thereby being identified as definitely lateral structures, while the lateral ventricle of the cerebral hemisphere, the recessus optici lateralis, and pineal outgrowth of each side originating in the latero-dorsal segment of the brain-wall dorsal to the sulcus limitans are definitely dorsal structures.

The *sulcus medius* diverges from the sulcus limitans in the diencephalic region and passes rostro-dorsally to disappear just latero-ventrad of the definitive neuropore (recessus neuroporicus internus). In the proximal part of its course it divides, on the wall of the diencephalon, a larger dorsal from a smaller ventral eminence, these being the anlagen of the pars dorsalis thalami and pars ventralis thalami.

The *sulcus ventralis* runs forward from the caudal region of the hypothalamus, forms the rostro-ventral boundary of the pars ventralis thalami, intersects the sulcus limitans, and disappears just ventrad of the thickened middle part of the lamina terminalis.

The less conspicuous *sulcus dorsalis* traverses rostrally the dorso-lateral wall of the synencephalon and the diencephalon, divides the epithalamus from the pars dorsalis thalami, and

disappears on the wall of the telencephalon slightly laterad of the recessus neuroporicus internus.

Stage K.

Embryo No. 39 was examined and modelled (Pl. III. fig. 14).

Telencephalon.

The secondary telencephalon has undergone extensive dorsal and rostral development, the thinned roof of the primary telencephalon now being represented by the narrow infold of tissue at the bottom of the deep furrow separating the developing hemispheres.

Diencephalon.

The roof is now a prominent dome, the first indication of the dorsal sac. The eminence on the lateral wall of the neuromere is more clearly defined and like the recessus thalami prænuclearis, whose position it indicates, is it now assuming a definitely conical form. The primary optic vesicle exhibits on its lateral surface an oval depression—the beginning of the invagination which ultimately results in the formation of the optic cup.

The *Synencephalon* is large and is separated from the diencephalon and the mesencephalon by deep external furrows and correspondingly conspicuous internal constrictions. On each of its lateral walls appears the well-marked conical eminence which is the external expression of the deep recessus geniculi.

Since this pair of recesses obviously belong to the fore-brain the apparent difficulty referred to by Dendy (1910, p. 249 footnote) disappears.

The primary epiphysial outgrowth appears as a small, oval, thin-walled evagination of the roof of the synencephalon. It is situated slightly to the left of the mid-dorsal line, and its rostral border is immediately caudad of the di-synencephalic boundary.

Stage L.

Embryo No. 50 was examined and modelled (Pl. IV. fig. 15).

Telencephalon.

The developing cerebral hemispheres are more rounded and prominent than were those of the embryo previously described, and rostro-ventrad of each of them is a clearly defined low rounded eminence corresponding to the recessus preopticus lateralis. The paraphysial arch is more convex and does not extend so far laterally as it did during Stage K, the rudiment of the paraphysis therefore being more clearly defined. The primitive optic vesicle has become more spherical and deeply cupped, and the optic stalk more constricted and circular in cross-section.

Synencephalon.

The pineal outgrowth is now transversely constricted into a spherical anterior and a pyriform posterior portion, the cavities of these being continuous with one another and with that of the synencephalon.

In other respects the fore-brain of this embryo is very similar to that of the embryo of Stage K.

Chick embryo of 72 hours.   (Pl. VIII. figs. 33 & 34.)

In respect of the structures now under consideration the stage of development reached in this embryo appears to be very similar to that of *Sphenodon* during Stage L. In both cases the three neuromeres of the fore-brain are clearly differentiated, and the members of the two series of diverticula of the brain-cavity are practically identical in position and degree of development in the two embryos. The cerebral hemispheres appear to be somewhat more clearly differentiated in the Chick, their somewhat less developed condition in the *Sphenodon* embryo probably being an indication of the more primitive nature of that animal.

Stages N and O.

Stage N, Embryo No. 14 *a* was examined and modelled (Pl. IV. figs. 16, 17, and 18).

Stage N-O, Embryo No. 24 *a*, and Stage O, Embryo No. 92, were examined.

There is so little difference between these embryos that for the present purpose they may conveniently be considered together.

Telencephalon.

In Embryo No. 14 *a* (Pl. IV. figs. 16 & 17) each of the paired secondary telencephalic evaginations is large, clearly defined and hemispherical, and the name "cerebral hemisphere" may now be justly applied to them. They are separated rostrally by a shallow fold of ependyma, which passes caudally into a low, convex, and gradually widening ridge, the tela choroidea, which here constitutes the persistent primary telencephalic roof-plate (Pl. IV. fig. 18), and from the caudal end of which rises the short, blunt, dorso-caudally directed tubular paraphysis. A slight infolding of the lateral border of the tela choroidea occurs at its junction with the thick wall of the cerebral hemisphere. This is the rudiment of the *choroid plexus of the lateral ventricle* (plexus hemisphærium, Gisi), and immediately lateral to it a transverse section of the medio-dorsal wall of the hemisphere exhibits a primitive hippocampus with an outer cell-free zone and a narrower matrix crowded with cells. The floor of the telencephalon and the lamina terminalis are considerably thinner than in younger embryos. The recessus ventricularis, preopticus

medius, preoptici laterales, and postopticus are well developed, and nerve-fibres are appearing in the commissura anterior. A thickening in the velum transversum apparently represents the developing commissura aberrans.

Diencephalon.

The cavity of the primitive optic vesicle is much reduced and communicates with that of the diencephalon by the narrow cavity of the optic stalk, which now projects at right angles to the brain-wall. The stalk-cavity is constricted distally and its wider proximal half shows a considerable caudal expansion. The roof and walls of the dorsal sac are reduced to thin ependyma, but a transverse thickening of the extreme caudal part of the roof indicates the position of the commissura superior, in which nerve-fibres are beginning to develop. The recessus thalami prænuclearis and the external eminence corresponding thereto are conspicuous, and a transverse section in this region shows the presence in the wall of the diencephalon of a small lateral fore-brain tract, also of an oval patch of dense tissue which is probably the optic nucleus, and of a small ventro-lateral fibre tract, presumably the tractus striato-hypothalamicus.

Synencephalon.

The recessus geniculi is deep and well-defined and its corresponding external eminence is still conspicuous, and a transverse thickening forming the caudal boundary of the roof of the synencephalon indicates the developing commissura posterior.

In Stage N the epiphysis shows slight differentiation into a narrow proximal stalk and a slightly dilated rostro-dorsal extremity, and in Stages N -O and O the distal portion of the epiphysis has divided into a rostral vesicle (morphologically left, Dendy 1910), which ultimately becomes the pineal eye, and an immediately caudal (morphologically right) pineal sac which is attached to the roof of the synencephalon by the hollow pineal stalk.

Chick embryo of 96 hours.   (Pl. VIII. figs. 35 & 36.)

In the brain of this embryo the extent and relative positions of the diverticula of the central cavity, and the degree of histological differentiation in the brain-wall are very similar to those in Sphenodon embryos of Stages N and O.

Stage P.

Embryos Nos. 39 a and 45 a were examined, and the latter was modelled (Pl. IV, fig. 19; Pl. V. figs. 20, 21).

During the period between Stages O and P the development of the brain has considerably progressed, its general dimensions have approximately doubled, and its constituent neuromeres have become much more clearly defined.

Telencephalon.

The cerebral hemispheres have undergone great rostro-ventral elongation, each of them having assumed a somewhat laterally flattened pyriform shape, the long conical ventro-rostral extremity being the newly-developed olfactory peduncle, moderately thick-walled, and containing a conical extension of the secondary telencephalic cavity. The lamina neuroporica forms a stout bridge uniting the central of the medial walls of the cerebral hemispheres, the tela choroidea is in process of conversion into the septum ependymale, and the lateral extremities of the still wide foramen interventriculare have undergone some constriction, suggesting the first appearance of definite foramina of Monro. The latero-ventral sector of the wall of the fore-brain has undergone enormous thickening throughout almost the whole length of the cerebral hemisphere, this being most pronounced in the middle third of its course, and a similar but less conspicuous thickening has occurred in the dorso-lateral and medio-ventral sectors. The first and second of these thicken-ings constitute respectively the *palœostriatum* and the *hypo-pallium*, which are separated by the sulcus interstriatilis, a conspicuous angulus ventralis being included between the hypo-pallium and the third or medio-ventral septal thickening (Pl. VI. fig. 24). The comparatively thin dorsal and dorso-lateral sectors contain respectively the primitive hippocampus and the general pallium. The sulcus superstriatilis is not very conspicuous. The paraphysis is a dorso-caudally directed tube with transversely folded thin walls, and lies against the rostral surface of the roof of the dorsal sac. The velum transversum, and the rudiment of the choroid plexus of the lateral ventricle of each of the cerebral hemispheres are more conspicuous (Pl. VI. fig. 25), and the *commissura aberrans* is well developed.

Diencephalon.

The distal half of the cavity of the optic stalk is obliterated, the proximal half containing the recessus optici lateralis being still much dilated, a marked convexity of its rostro-ventral surface clearly defining the position of the recess, caudad of which the wall of the stalk is distinctly thickened. The optic chiasma appears to be extending dorsally and caudally, thus producing an apparent change in its position relative to the recessus optici lateralis, which now appears to be sited rostrad and slightly dorsad of the chiasma instead of caudad, as in the earlier stages of development. Since Stage O each optic stalk has undergone ventral rotation through an angle of more than 60°, so that they now diverge at an angle of about 45°, and their solid distal extremities are caudally deflected. The laterally flattened recessus preopticus medius is very deep and large in this embryo. The dorsal sac is more than twice as long in each direction as it was in Stage O, and its cavity is more constricted-off from that of the diencephalon by the much thickened pars

dorsalis thalami. The recessus thalami prænuclearis is a deep, sharply-pointed, triangular-based pocket (Pl. V. fig. 20); the infundibulum is large and the sulcus ventralis persists only in the centre of its wall, where it forms a somewhat conspicuous recess.

Synencephalon.

With the exception of a short proximal vestige the cavity of the pineal stalk is obliterated, and the recessus geniculi (Pl. V. fig. 20) is large, deep, and triangular in cross-section, its caudal border being somewhat prolonged.

Stage P–Q.

Embryo No. 51 *a* was examined and modelled (Pl. V. fig. 22 ; Pl. VI. figs. 23, 24, 25).

Telencephalon.

The cerebral hemispheres have more closely approximated to the adult form, the stout-walled olfactory peduncles having elongated and straightened rostrally, and have developed bulbous extremities into which the lateral ventricles extend. The dorso-lateral surface of the caudal half of each hemisphere is more massive and rounded owing to the increased thickness of the neopallium, just laterad of which the pyriform lobe has appeared. Between the conspicuous sulcus and the lateral surface is the lateral fore-brain tract, which seems to originate slightly rostro-dorsad of the commissura anterior, some of the fibres of which appear to enter the tract, and it can be traced caudally into the floor of the hypothalamus and thence into that of the mesence-phalon. Immediately latero-ventrad of this tract is the lateral olfactory tract, which appears to originate laterad of the former and to terminate in or near the habenular ganglion. The wall of the hemisphere exhibits an external mantle-layer, a thick cortex, and a narrow matrix, the first of these disappearing in the ventral and medial sectors (Pl. VI. fig. 24).

Diencephalon.

The dorsal sac is much expanded laterally, the recessus optici lateralis is further reduced, and the recessus thalami prænuclearis is deeper and narrower, mainly owing to the increased thickness of the thalamus, in which the nucleus thalami anterior has developed immediately rostro-dorsad, and the nucleus rotundus caudo-dorsad of the recess. Ventrad of the nucleus thalami anterior is the caudal portion of the tractus thalamo-striatilis, which runs from the latero-caudal region of the telencephalon into the descending tract of the mesencephalon and myelence-phalon. A number of small irregular infoldings of the ependymal roof of the dorsal sac project downwards into its cavity. These are the rudiments of its choroid plexus, the structure of which in the adult has been described by Dendy (1910, p. 253).

Synencephalon.

The recessus geniculi is now deeper, narrower, and triradiate in cross-section, and the fasciculus retroflexus (tractus habenulo-peduncularis, or bundle of Meynert) from the caudal region of the habenular ganglion curves rostro-ventrally round the recess, passing between it and the nucleus rotundus, then caudo-ventrally into the floor of the mesencephalon below the optic lobes, where it becomes practically indistinguishable from the tractus tecto-bulbaris and appears ultimately to decussate.

Stage Q.

Embryo No. 52 *a* was examined and modelled (Pl. VI. fig. 26).

Few further developmental changes are to be observed. The olfactory bulbs are considerably enlarged, and the olfactory fibres may be roughly divided into a dorso-lateral and a ventro-medial group, and on the dorso-medial surface of each olfactory bulb is a large ovoid accessory bulb (the formatio vomero-nasalis, Zuckerkandl, 1910), which is about one third as large as the former (see Stage R, Pl. VII. fig. 27). It may be noted that *Chrysemys* has a similarly situated accessory bulb nearly equal in dimension to the olfactory bulb (McCotter, 1917). I was unable to detect the presence of a definite nervus vomero-nasalis, but in Stage R a number of fibres from the accessory bulb certainly run caudad into the dorsal and ventral lateral olfactory tracts. Slightly rostrad and dorso-laterad of the recessus preopticus medius a group of ganglion cells are present in the wall of the hemisphere, and these I believe to be the ganglion terminale, from which a fine strand of nerve-fibres run forward and appear to emerge from the ventro-medial surface and pass into the septum between the olfactory peduncles. Further than this I could not certainly trace them, but on the medio-dorsal surface of the olfactory bulb a similar strand of fibres could be detected and traced into the latero-ventral wall of the nasal sac, and I believe that these fibres represent the nervus terminalis. If this be so, the olfactory nerve and the nervus terminalis may be considered to represent the separated components of the primitive segmental nerve of the telencephalon (Neuromere I), as suggested by Johnston (1913).

The plexus of each lateral ventricle is larger and has begun to invade the foramen of Monro, their median portion remaining within the foramen interventriculare. There is no plexus medialis as described by Gisi (1907).

The recessus thalami prænuclearis is digitate with a wide funnel-shaped mouth, and the recessus geniculi is T-shaped in cross-section, the long branch of the T being caudally directed to form a deep sulcus which gradually shallows and disappears in the caudal part of the iter. The commissura posterior is much more conspicuous than it was in younger embryos.

Chick embryo of 144 hours.

This appears to have reached a stage of development approximately equivalent to that of *Sphenodon* Stage Q. Its general morphology is indicated in Pl. IX. figs. 37 and 38.

Stages R, S, and adult *Sphenodon*.

Embryos Nos. 141, 142, and 162 of Stage R, 9* and 11* of Stage S, and adult *Sphenodon* Nos. I., II., and VI. were examined.

Stage R, No. 162 was modelled (Pl. VII. figs. 27, 28, 29).

During and after Stage R the fore-brain of *Sphenodon* exhibits the general shape and structure of the adult condition, which has been described and figured by Gisi (1907), while Dendy has given figures of Stage S (1910, fig. 44) and of the adult brain (*id.* fig. 12, and text-fig. 1). It has therefore been considered unnecessary to give a detailed description of the brain during these concluding stages of development, especially as an exhaustive account of the morphology of many of its components has been given by Dendy (1910) and Wyeth and Row (1923). The salient features are indicated in Pl. VII. figs. 27, 28, 29, and 30, and details of only those structures with which the present investigation is specially concerned, or features which have formerly been adequately described are now given.

Telencephalon.

Since Stage Q the hypopallial eminence has considerably developed and now forms a bold convex floor to the lateral ventricle. Its dorsal surface is semi-pyriform, extending in a continuous sweep from the ventro-caudal extremity of the ventricle into the middle third of the peduncular region (Pl. VII. fig. 28),—an undoubtedly primitive feature, since in the higher Vertebrates it is mainly confined to the caudal half of the hemisphere. A continuous well-defined layer of cortical cells (*c.c.* Pl. VII. fig. 31) is present just below the dorsal surface of the eminence, to the contour of which it conforms, as first demonstrated by Elliot Smith (1919),—another primitive feature, since in the higher Vertebrates these cortical cells are diffused, no clear continuous layer being present. The zona intermedia of the palæostriatum has disappeared, but in the dorso-medial sector of the wall of the hemisphere there is a well-defined cortex and a narrow matrix. Immediately ventral to the angulus ventralis is a semilunar nucleus accumbens of Kappers, and ventral to this a somewhat similar cell-mass, the tuberculum olfactorium (Pl. VII. fig. 30). Immediately lateral to the nucleus medianus septi is the nucleus lateralis septi, and in the caudal region of the hemisphere ventro-lateral to the sulcus interstriatilis is the large nucleus ventro-medialis, just dorso-lateral of which is the tractus olfactorius lateralis. In the medial wall of the hemisphere at the level of the recessus thalami

prænuclearis is the large nucleus commissuræ aberrantis situated at the dorso-lateral extremity of the commissure. Immediately surrounding the recessus preopticus medius is the nucleus preopticus (Pl. VII. fig. 31), and lateral to this is the lateral fore-brain tract.

Hines (1923) describes a number of additional nuclei and nerve tracts, which, possibly owing to lack of suitably stained sections, I have been unable to detect.

Owing to the great development of the hypopallial eminence the lateral ventricle is much reduced. The cavity is semilunar in cross-section and its general contour is like that of half a pear, its tapering rostral portion being much elongated as the cavity of the olfactory peduncle, and terminating in the ovoid cavity of the olfactory bulb. The paraphysis is a long, dorso-caudally directed tube closely apposed to the anterior wall of the dorsal sac, its cylindrical lumen exhibiting a number of radially disposed crypt-like diverticula resulting from the longitudinal folding of the tube, between which are a number of blood-lacunæ, the whole organ being enclosed and bound to the wall of the dorsal sac by the pia mater (Dendy, 1910). The recessus preopticus lateralis of each side is still evident as a small rounded pocket in the mid-lateral wall of the large recessus preopticus medius.

Diencephalon.

The recessus optici lateralis of each side has undergone a further slight reduction in size and is a small cylindrical diverticulum diverging from its fellow at an angle of nearly 90°, and is situated immediately dorsad of the rostral border of the optic chiasma. In Stage S, and in the adult, the recess is still further shortened, and its distal extremity forms a small vesicular dilatation situated just above the point at which the antero-lateral extremity of the optic chiasma leaves the brain. Externally its position is indicated by a low rounded projection on the surface of the brain in the angle between the cerebral hemisphere and the rostral border of the optic chiasma. The recessus thalami prænuclearis in Stage R lies in the substance of the thalamus at the level of the middle of the recessus preopticus medius, and is situated ventrad of the conspicuous commissura aberrans and slightly caudad of the foramen of Monro. The recess is a horizontal digitate diverticulum with a slightly expanded proximal and a rounded vesicular distal extremity, and is directed caudally at an angle of 60°. In Stage S, and in the adult, its position is unchanged, but its long axis is at right angles to the ependymal surface of the third ventricle, and only its more conspicuously dilated distal third is directed caudally as in Stage R. Its ependyma is composed of tall columnar cells and is thrown into folds, these being most conspicuous in the distal part of the recess, thus giving its cavity a radiate cross-section.

Synencephalon.

As the pineal outgrowths have been fully described by Dendy (1899 *b* and 1910), only their salient features are now given.

In Stage R the pineal eye has assumed its adult external form as a conical vesicle, the rounded base of which lies just ventral to the parietal plug. From its proximal apical portion the left nervus pinealis passes ventro-caudally, along the ventral surface of the pineal sac, and thence apparently into the left habenular ganglion, some of its fibres apparently entering the commissura superior (Dendy, 1910). The pineal sac in Stage R is approximately pyriform, lies on the posterior wall of the dorsal sac with its vertex caudally directed, from which the pineal stalk (tractus pinealis) passes ventrally and caudally to open into the third ventricle by the funnel-shaped recessus infra-pinealis situated between the commissuræ superior and posterior. The cavity of the stalk persists in only a short part of its proximal region. In Stage S the pineal sac is folded in a V-shape, and in the adult the distal limb of the V tapers into a rostral conical diverticulum lying dorsad of the dorsal sac and the paraphysis. The widest part of the sac lies in the vertex of the V, and its proximal part tapers abruptly into the tractus pinealis which lies against the caudal surface of the dorsal sac and opens into the third ventricle as in Stage R. The fibres of the right nervus pinealis pass into the right habenular ganglion and Dendy has also traced them into the commissura posterior, which owing to its recent rapid growth now projects into the third ventricle and exhibits a transversely folded appearance, the sub-commissural organ being conspicuous along its ventral surface. The large habenular ganglia bulge inwards and upwards, their posterior parts meeting above the commissura superior, and from each of them a bundle of Meynert passes ventro-caudally rostrad of the recessus geniculi.

A detailed description of these structures is given by Dendy (1910). The recessus geniculi lies immediately caudad of the nucleus rotundus, ventro-caudad of the habenular ganglion, and ventrad of the commissura posterior. It is now a deep, narrow, slightly ventrally directed diverticulum, from the caudal side of the base of which runs a shallow dorso-caudal sulcus, forming a lateral wing of the iter and disappearing at the rostro-ventral border of the optocœle. In the adult the rostro-ventral deflection of the conspicuous distal part of the recess, and the folded appearance of the ependymal epithelium are more pronounced. The eminences on the external surface of the brain, which in the earlier stages of development indicated the positions of the recessus geniculorum and the recessus thalami prænucleares, have now disappeared.

Chick embryo of 192 *hours.*

This is shown in Pl. IX. figs. 39, 40, and 41. In respect of its neuromeric segmentation, and the differentiation of the diverticula of its central cavity, the brain of this embryo appears to be very similar to that of *Sphenodon* Stage R. In the brain of a Gecko embryo of approximately the same stage of development as *Sphenodon* Stage S these diverticula were found to be somewhat smaller, but similar in situation and general relationship to the adjacent structures.

5. THE SERIAL HOMOLOGY OF THE PAIRED RECESSES.

Dendy (1910) demonstrated the presence,—in addition to the lateral ventricles of the cerebral hemispheres, the cavities of the pineal outgrowths and those of the optic lobes,—of three pairs of lateral diverticula of the central cavity of the brain of *Sphenodon*. He named these the recessus optici laterales, the recessus thalami prænucleares, and the recessus geniculorum. He then advanced the two suggestions:—(1) that all these pairs of outgrowths of the neural tube are homologous with one another, and (2) that each pair belongs to an originally separate neuromere. It is necessary now to consider the facts concerning the development and morphology of the diverticula of the central cavity of the fore-brain which have been elicited during the present investigation, and to discuss their application to these suggestions.

(A) *The Lateral Ventricles of the Cerebral Hemispheres.*

It is universally accepted that the cerebral hemispheres of Vertebrates originate as paired evaginations of the dorsal zone of the telencephalon (Johnston, 1919). In *Sphenodon* they first appear in embryos of late Stage J, and if judged by the organogeny in general this is rather late compared with their appearance in higher Vertebrates, although even in the latter they appear later than do the primitive optic vesicles. Their relatively late appearance in *Sphenodon* may therefore be a primitive feature, and the fact that the caudal slightly precedes the rostral part of the evaginations in respect of the time of its development is reminiscent of the condition obtaining in early embryos of Batrachia, and may perhaps be similarly interpreted. During Stage K the development of the hemispheres proceeds most rapidly in the rostral region, and until the end of Stage O each hemisphere increases rapidly in size and is of clearly defined hemispherical shape. The size and shape of each of the lateral ventricles closely conform to those of its hemisphere, and it communicates with its fellow by means of the wide median or common ventricle (foramen interventriculare of Pl. VI. fig. 25), the lateral constrictions of which producing the foramina of Monro are of late occurrence (Stage Q). The lateral ventricle

attains its maximum size relative to that of the whole brain during Stages O–P, after which period the appearance and rapid development of the hypopallial eminence (Hunter's ridge) causes a considerable diminution of its cavity, until the much-reduced condition obtaining in the adult brain is produced. This eminence extends uninterruptedly from the extreme ventro-caudal part of the ventricle into the caudal third of the peduncular region (Stage R, Pl. VII. fig. 28), while, as Elliot Smith (1919) points out, its characteristic band of cortical cells (Pl. VII. fig. 31) may be traced even further forward, both of these features being more primitive than the more caudal localisation of the hypopallium and the diffusion of its cortical cells which occur in the brain of higher Vertebrates. That the cerebral evagination occurs near the dorsal extremity of a short vertical sulcus situated on the wall of the primary telencephalon in Stages J and K has already been stated, and this sulcus has been homologised with the sulcus limitans hippocampi of Selachians and Batrachians described by Johnston (1911), and must evidently be regarded as the primitive neuromeric groove of the telencephalon.

(B) *The Recessus Preoptici Laterales.*

This pair of recesses appear to have escaped the attention of earlier observers, possibly in part because during no stage of development are they very large or conspicuous, but mainly because the existence of even a single series of diverticula remained un-suspected until its presence was suggested by Professor Dendy. It may, however, be noted that Warren (1911) indicates but does not name one of these recesses in a *Lacerta* embryo in his fig. 7, and it is shown more distinctly in *Chrysemys* embryos in his figs. 20, 21, and 22. I have also observed these recesses in Chick embryos of three to six days inclusive.

The recessus preopticus lateralis of each side first appears in embryos of early Stage J as a small rounded pocket in a wall of the primary telencephalon at the point of intersection of the sulcus limitans and the primary telencephalic groove. It is therefore considerably ventrad of the level at which the cerebral evagination subsequently appears, and its position rela-tive to the sulcus limitans clearly indicates that it is a lateral structure.

The recessus preoptici laterales are therefore to be regarded as the rostral pair of members of a series of metamerically arranged lateral diverticula of the central cavity of the fore-brain, of which series the recessus thalami pronucleares and the recessus geniculorum are homologous and more caudal members. They persist during the whole period of development included between Stages J and Q, and like the other paired diverticula now under consideration they first undergo a considerable increase of size, but are much reduced during the concluding stages of development.

They attain their maximum dimensions during Stage L (Pl. IV. fig. 15), at which period the position of each of them is indicated by a conspicuous rounded eminence on the external surface of the wall of the telencephalon slightly ventrad of the rostro-ventral border of the developing cerebral hemisphere. Until Stage P (Pl. V. fig. 20) they are fairly conspicuous, but undergo considerable reduction in Stage Q, while in Stage R they are hardly distinguishable (Pl. VII. fig. 28).

(C) *The Recessus Optici Laterales.*

It has already been mentioned that earlier writers appear implicitly to have accepted the fact that the recessus optici laterales are the persistent proximal vestiges of the cavities of the primitive optic vesicles, and the present investigation has established this beyond doubt in the cases of *Sphenodon* and the Chick. Von Kupffer (1906) assumed them to be ventral structures, and on this ground he refused to accept the lateral eyes as structures serially homologous with the pineal outgrowths; and Warren (1911), in describing the development of the fore-brain of *Lacerta* and *Chrysemys*, states that the lateral eyes develop as a pair of ventral evaginations of the cavity of the first neuromere or telencephalon. Johnston (1906) had previously asserted that the optic vesicles are derived from the dorsal zones of the second neuromere or diencephalon, and that they occur on the course of the primitive optic groove. This view, which has since been generally accepted, is confirmed by the results now recorded. In *Sphenodon* the rudiments of the primary optic vesicles first appear during Stage E as a pair of small oval thickenings of the dorsal border of the lateral wall of the diencephalon (Pl. I. fig. 2). During Stages F and G they greatly increase in size and become distinctly vesicular (Pl. I. fig. 5 ; Pl. II. figs. 6, 7, & 8). During Stage H they are very conspicuous as a pair of large, nearly hemispherical evaginations of the dorso-lateral wall of the diencephalon, and in Stage J they are much more clearly defined, especially around the caudal part of their periphery (Pl. III. fig. 11). The wide aperture by which the cavity of each of them communicates with that of the fore-brain is situated caudad of the di-telencephalic groove, and dorsad of the sulcus limitans, and this establishes the fact that the primary optic vesicles are paired evaginations of the dorsal zone of the rostral region of the wall of the diencephalon.

Although morphologically dorsal, the lateral eyes ultimately assume a topographically ventral position apparently owing to the enormous development of the dorso-lateral region of the fore-brain which subsequently takes place. Johnston (1908) gives an explanation of the apparent ultimate ventrality of the lateral eyes which, it appears to me, receives some support from the fact that I have now observed during Stages K–N the

occurrence of a somewhat thinner tract in the wall of the diencephalon, extending from the dorso-lateral region to a point just dorsad of the base of the optic stalk. Until Stage P is reached the aperture by which the stalk-cavity,—which has undergone progressive centripetal closure during Stages M-O and may now be called the recessus optici lateralis—, communicates with that of the fore-brain is dorsal to the caudal surface of the chiasma ridge. The proximal part of the stalk-cavity still exhibits a distinct, but diminishing, caudal extension along the lateral wall of the diencephalon, the diencephalic origin of the recess thus being evident throughout the whole period of development included in Stages E-P. During Stage P there occurs in the caudally deflected distal half of the optic stalk a considerable development of nerve-fibres, which pass caudad of the recessus optici lateralis and enter the optic chiasma. The last-named structure also undergoes considerable thickening, especially along its caudal surface which is thus shifted further caudad, while its dorsal extension slightly displaces the recess in the dorso-rostral direction. This produces the appearance noted in embryos of Stages R and S, in which the recessus optici lateralis is found to be still further reduced in depth, to diverge from its fellow at an angle of nearly 80°, and to be situated immediately dorsal to the rostral surface of the optic chiasma. In the adult the recess is found to have undergone little further reduction, and to have been still further dorsally and rostrally displaced, apparently owing to increased development of nervous tissue in the region of the junction of the optic nerve with the chiasma.

From the foregoing observations it is clear that no true conception of the relationships and neuromeric value of the recessus optici laterales could result from an examination of only the later embryos or of adult *Sphenodon*. The conditions obtaining in these suggest that the recesses are paired ventral diverticula of the central cavity of the telencephalon, whereas their earlier developmental history clearly proves them to be dorsal and diencephalic in origin. In this connexion it may be noted that the dorsal and caudal extension of the commissural nerve-fibres of the optic chiasma in *Sphenodon* is by no means unique, for a similar phenomenon may be observed in the Chick, while Warren (1911) records a similar caudal extension of the posterior commissure in late embryos of *Lacerta* and *Chrysemys*, and I have observed the same process in those of *Sphenodon* and the Chick. That the retinal elements of the lateral eyes are derived from the diencephalon, while the fibres of the optic nerve by means of which they make intra-cerebral connexion with the optic lobes, enter the optic chiasma, a structure belonging to the telencephalon or neuromere next rostral to the diencephalon, will again be referred to in discussing the homology of the pineal outgrowths with the lateral eyes.

(D) *The Recessus Thalami Prœnucleares.*

Except for the possible reference to one of these recesses in the brain of *Sphenodon* by Gisi (1907, p. 47), quoted above, they appear to be have been unnoticed, until described by Dendy in Stages R, S, and adult *Sphenodon.* During the present investigation I have found them in embryos of the Chick, in which, both in respect of their appearance and development, they are similar to those of *Sphenodon* (*cf.* Rendahl, 1924, figs. 39, 40, "Segment-hohle das Parencephalon"). They are also present, although somewhat smaller, in a Gecko embryo of a stage of development approximately equivalent to *Sphenodon*, Stage S. In the preceding section of this paper it has been shown that the recessus thalami prænucleares are the persistent vestiges of the pair of lateral diverticula of the central cavity of the diencephalon. Each of them appears during early Stage J as a dorso-ventrally elongated oval pocket in the wall of the diencephalon, immediately caudad of the primitive optic vesicle. The deepest and central part of the recess is situated in the lateral zone of the wall at the point where the sulcus limitans intersects the primitive diencephalic groove. The latter extends from a point immediately caudad of the velum transversum into the primitive infundibular recess or recessus postopticus (Kingsbury, 1922), and its ventral portion is probably identical with the sulcus hypothalamicus of Johnston (1911). During Stages K–O the recessus thalami prænuclearis gradually assumes a conical form, its proximal part becoming narrower owing to the encroachment of the partes dorsalis and ventralis thalami. During Stages P-Q it becomes still further constricted owing to the development of the nucleus thalami anterior rostrad, and of the nucleus rotundus caudad of its cavity. The further development of these thalamic structures during Stage R causes the recess to assume a digitate form, its distal extremity remaining somewhat enlarged, the only subsequent alteration of its structure being the development of a number of longitudinal folds of its ependyma, thus giving its cavity a radiate cross-section.

(E) *The Pineal Outgrowths.*

A detailed account of the development of the pineal outgrowths was given by Dendy (1910), whose results I have confirmed, while the bilateral development of these organs in the Chick has been demonstrated by Cameron (1903-4). Dendy (*op. cit.* pp. 308–313) gives a very complete summary of the results obtained by earlier investigators, and he conclusively proves that in *Sphenodon* these outgrowths originate as a pair of dorsal diverticula, and therefore that they belong to the same neuromere. The primary pineal vesicle arises very slightly to the left of the middle line during Stage K, its segmentation begins during Stage L, and complete separation of the two resultant

vesicles occurs during Stages N and O. It remains only, there-
fore, to consider the grounds for the present assumption that
they belong to the synencephalon. Johnston (1906) assigns the
anterior epiphysial outgrowth to the third, and the posterior
epiphysial outgrowth to the fourth neuromere, *i. e.*, to the synen-
cephalon and to the first neuromere of the mid-brain respectively.
In view of the results obtained by Hill, Cameron, and Dendy,
and of those now recorded, this suggestion is obviously untenable.
Warren (1911), on what appear to me to be quite inadequate
grounds, assigns the two pineal outgrowths to the second
neuromere, *i. e.* to the diencephalon, which he calls the paren-
cephalon ; but in the case of *Chrysemys* his figs. 19 and 20 are
inconclusive, while his figs. 21, 22, and 23 of *Chrysemys* and
figs. 5 and 6 of *Lacerta* strongly suggest a synencephalic origin
for these outgrowths. In the case of *Chelydra* (Johnston, 1913,
figs. 3, 4, and 5), and of the Human embryos described by Hines
(1922, figs. 14, 15, and 18), it would appear that the pineal
outgrowths arise from the synencephalon. Dendy has shown
that in *Sphenodon* the central part of the cavity of the pineal
stalk persists as the recessus infra-pinealis, which is obviously a
part of the cavity of the synoncephalon, and that even in the
adult (*Sphenodon* VI.) the lower part of the tractus pinealis is
still open. My own models clearly show that the cavity of the
pineal stalk is continuous with the cavity of the synencephalon
until a late stage of development (Pl. V. fig. 20 ; Pl. VI. figs. 23,
26 ; Pl. IX. figs. 38, 40).

Further, Dendy suggests that the right and left nervi pineales
connect via the commissura superior with the habenular ganglia,
thus confirming Cameron's assertions respecting the same struc-
tures in the Chick. It will be noted that in entering the com-
missura superior, which belongs to the diencephalon or neuromere
next rostral to the synencephalon, the pineal nerves behave
similarly to the optic nerves which enter the optic chiasma, a
structure belonging to the telencephalon or segment next rostral
to that to which the primitive optic vesicles belong. This fact
seems to lend support to the suggested serial homology between
the recessus optici laterales and the cavities of the pineal
outgrowths, if, as it now appears, the recessus optici laterales are
correctly assigned to the diencephalon and the pineal outgrowths
to the synencephalon. It must therefore be concluded that the
pineal outgrowths are paired dorsal diverticula of the synence-
phalon and that their cavities are serially homologous with those
of the lateral eyes.

(G) *The Recessus Geniculorum.*

The developmental history of these recesses can hardly be
misinterpreted. In both *Sphenodon* and the Chick they arise
as large paired lateral diverticula of the central cavity of the
synencephalon, gradually assuming first a conical and finally a

triradiate shape. The development of the nucleus rotundus and Meynert's bundle rostrad, and of the nucleus thalami lentiformis caudad of each of these recesses define their position as lateral derivatives of the synencephalic cavity in the later stages of development as clearly as does the first appearance of the recesses. Dendy, who examined only comparatively late embryos and adult specimens of *Sphenodon*, was inclined to refer the recesses to the mid-brain, but he noted Elliot Smith's objection that the similarly-named recesses of the Mammalian brain are fore-brain structures (Dendy, 1910, p. 249, footnote). As the present investigation establishes the fact that these structures belong to the synencephalon, their homology with the recessus geniculorum of the Mammalian fore-brain is evident, and the difficulty referred to in Dendy's footnote disappears.

From the above discussion it is evident that the fore-brain of *Sphenodon* and of the Chick exhibits one dorsal and one lateral series of metamerically arranged diverticula of its central cavity. One pair of the members of each series has now been assigned to each of the three constituent neuromeres of the fore-brain.

It may be added that since the sulcus limitans is generally accepted as the line of demarcation between the primitive sensory dorso-lateral and primitive motor ventro-lateral zones of the brain-wall, it might perhaps be expected that those diverticula (*i. e.*, the lateral ventricles of the cerebral hemispheres, the recessus optici laterales, and the cavities of the pineal outgrowths) which constitute the cavities of the sensory organs (viz., the olfactory, optic, and pineal organs) would originate within the sensory zone of the brain-wall dorsad of the sulcus limitans. That they do so has now been demonstrated.

6. The Neuromery of the Fore-Brain.

Although nearly all recent writers on the neuromery of the Vertebrate brain agree in considering that although it passes through a stage of development when it exhibits three conspicuous vesicular dilatations, which they call the fore-, mid-, and hind-brain vesicles, yet during the immediately subsequent stages of development the fore-brain and mid-brain together can be shown to include five neuromeres. Some of these writers state that these or a similar set of neuromeres can be detected even earlier than the so-called " three-vesicle " stage. Three of the five neuromeres are usually assigned to the fore-brain, and two to the mid-brain, and those writers who reverse this ratio appear to have done so because they have failed to recognise the synencephalon or third neuromere as a fore-brain component.

Hoffmann (1885) in the Reptilia, and Orr (1887) in *Lacerta* found that subsequent to the three-vesicle stage neuromeres developed in the fore-brain, but both writers appear to doubt whether these are true and " primary " neuromeres. McClure (1890) found three fore-brain " encephalomeres " in *Amblystoma*,

Newt, and Chick, and noted that the third encephalomere was the smallest of the series.   This agrees with the results now obtained in *Sphenodon* and the Chick.   Waters (1892) in *Gadus* and *Amblystoma*, Hill (1899, 1900) in *Salmo*, Johnston (1909) in the Pig, Herrick (1892) in *Eutænia*, Locy (1894–5) in *Acanthias*, and Warren (1911) in *Lacerta* and *Chrysemys*, all agree in dividing the fore-brain into three neuromeres.

Zimmermann (1891) in *Mustelus*, Chick and Rabbit, and Neal (1898) in *Acanthias* found two neuromeres in the fore-brain and three in the mid-brain, but from an examination of their figures it is obvious that these writers have identified the synencephalon as the first mid-brain neuromere.   Von Kupffer (1903), Neal, McClure, Herrick, and Warren consider the fore-brain neuromeres to be secondary, and not strictly homologous with the mid-brain and hind-brain neuromeres, on the grounds that the fore-brain neuromeres are mainly dorsal structures of comparatively late appearance.   Locy, however, found three " primary " fore-brain neuromeres, including the synencephalon, these fusing later to form the single fore-brain " vesicle," and being ultimately traceable into the three fore-brain neuromeres which the foregoing writers called secondary.   Hill agreed with Locy in finding three fore-brain neuromeres in his earliest embryos, but concluded that these neuromeres disappeared when the fore-brain vesicle was formed, and that the three fore-brain neuromeres which subsequently appear are secondary, and not strictly morphologically equivalent to the first or " primary " set.   This view was adopted by Warren ; while Bartlemez (1923), who examined a number of Human embryos, found a prosencephalon which ultimately exhibited two fore-brain neuromeres, a mesencephalon of two neuromeres, and a rhombencephalon containing three primary " segments," the latter eventually consisting of seven hind-brain neuromeres.   He suggested that the secondary primary segment of the rhombencephalon was also the fourth or otic neuromere of the hind-brain, and identical with the structure which earlier observers had called the " hind-brain vesicle " because it was, at all early stages of development, much more conspicuous than the other hind-brain segments.

Rendahl (1924) found four neuromeres in the fore-brain of the Chick, and named them respectively, telencephalon, parencephalon anterius, parencephalon posterius, and synencephalon. The first of these or telencephalon and the fourth or synencephalon appear to be identical with those neuromeres which have now been similarly named in *Sphenodon* and the Chick, while his two parencephalic neuromeres are together equivalent to the single neuromere which I have now called the diencephalon.   As a result of a careful re-examination of numerous Chick embryos I still believe that the diencephalon represents a single neuromere. I could discern no trace of a furrow corresponding to Rendahl's " inter-parencephalic furrow " (p_1-p_2), nor of any histological differentiation of the brain-wall of this region such as would

indicate an inter-neuromeric boundary. Rendahl's figs. 39 and 40 appear to indicate that the " Segmenthohle das Parencephalon " shown therein is really the recessus thalami prænuclearis, and that the "parencephalon posterius" comprises that part of the diencephalon which lies caudad of this recess and rostrad of the synencephalon. It must further be observed that this so-called parencephalon posterius does not exhibit any paired diverticula of its central cavity such as the results now recorded would appear to require as an indication of the presence of a fore-brain neuromere. Rendahl has entirely failed to recognise the existence and important neuromeric significance of the serially homologous paired recesses described in the present paper. His fig. 40 does however indicate the presence of two recesses which certainly represent the recessus thalami prænuclearis and the recessus geniculi ; the former he calls Segmenthohle das Parencephalon, and the latter is unnamed.

The present investigation suggests that soon after its earliest appearance *the prosencephalon of* Sphenodon *divides into at least two neuromeres (Stages D-F), these being ultimately found to be the telencephalon and diencephalon, while during and after Stage G a third neuromere, the synencephalon, is present. The fore-brain of the Chick appears to comprise the same three neuromeres* ; and these conclusions agree with those recorded by a large number of earlier investigators of the Vertebrate brain.

It may further be suggested that in the case of *Sphenodon*, and possibly in other Vertebrata, the existence of a three-vesicle stage is apparent rather than real, this condition being simulated during a very short and early period of development by a masking of the segmentation externally, although internally it is much more conspicuous. During and after Stage G the existence of the three fore-brain neuromeres is indubitable. That they are true neuromeres morphologically equivalent to those of the mid-brain and of the hind-brain appears to be proved by their early appearance, and by the fact that, contrary to the assumption of certain earlier writers on the neuromery of the brain of other Vertebrates, they are not exclusively dorsal structures. Not only are they first differentiated on the floor of the fore-brain, but they have now been shown to pair each of dorsal and lateral components, viz. the paired diverticula of their central cavity with the external eminences corresponding thereto. If it be objected that the very early appearance of the fore-brain neuromeres is less evident in other Vertebrates, it must also be remembered that *Sphenodon* is admittedly a very primitive type, and it is tempting and perhaps reasonable to suppose that the conditions exhibited therein in respect of these neuromeres may possibly be more primitive than the conditions obtaining in other Vertebrate brains.

A brief consideration of each of these three definitive or secondary fore-brain neuromeres may now be given.

Neuromere I—TELENCEPHALON.

This is defined caudally by Johnston's "di-telencephalic boundary" extending on each side from the lateral border of the caudal surface of the velum transversum to the caudal surface of the chiasma ridge. An internal dorso-ventral groove, Johnston's primary neuromeric groove 1, homologous with the sulcus limitans hippocampi of Selachians and Amphibians, marks the region of maximum lateral development of its cavity, and on the dorsal part of the course of this groove, during Stages K–O are developed the secondary telencephalic evaginations, or cerebral hemispheres, between which lies the persistent vestige of the dorsal part of the primary telencephalon, now reduced to an ependymal fold. The lateral ventricles of the cerebral hemispheres are paired dorsal diverticula of the cavity of this neuromere. A small pair of lateral diverticula, the recessus preoptici laterales, are developed, Stages J–P, further ventrad on the course of this groove. The recessus preopticus medius, which is conspicuous until Stage R, may possibly be regarded as the ventral member of this set of diverticula, and in it the primary telencephalic groove terminates. The olfactory nerves are the special sensory nerves, the pallium is the central part, and the nervi terminales are the peripheral part of the general cutaneous division of the somatic sensory nerve-components of the neuromere, as suggested by Johnston (1905).

Neuromere II—DIENCEPHALON.

On the internal neuromeric groove of this neuromere, Johnston's primary neuromeric groove II, are developed antero-dorsally the primary vesicles of the lateral eyes, the cavities of these undergoing rapid increase of size which is followed by progressive reduction in the later stages of development, and being ultimately represented by the small recessus optici laterales, as described by Dendy (1910), in Stages R, S, and adult *Sphenodon*. They appear earlier in development (Stage E) than do the corresponding diverticula of the other fore-brain neuromeres (Stage J). During Stage J the lateral diverticula of the cavity of this neuromere appear near the middle of the neuromeric groove of each side, and become the recessus thalami prænucleares. In an earlier paper (Wyeth and Row, 1923) the development of the hypophysis and its relation to the infundibulum have been described. The optic nerves are obviously the special sensory nerves of this neuromere, and it has been shown that Warren (1911) was obviously wrong in assigning the lateral eyes to the telencephalon, and in describing them as ventral structures. The posterior boundary of the floor of this neuromere is indicated by the tuberculum posterius. The primitive neuromeric groove of this neuromere terminates ventrally in the primitive infundibulum, which persists as the

recessus postopticus, while the definitive infundibulum with which the hypophysis connects appears to be a secondary evagination, as stated by Johnston (1919) and Kingsbury (1922) in Selachians.

Neuromere III—Synencephalon.

This is the smallest, and possibly slightly the latest formed of the fore-brain neuromeres, and does not become conspicuous until early Stage J, although its internal boundaries can be observed during Stage G. Its floor is bounded rostrally by the tuberculum posterius and caudally by the low ridge formed by the vertex of the habenular flexure, between which is included the post-tubercular recess. The recessus geniculorum are the lateral diverticula of the cavity of this neuromere, while the pineal outgrowths contain a pair of dorsal diverticula. These organs were shown by Dendy (1910) to be paired dorsal outgrowths of this neuromere, their cavities being serially homologous with the lateral ventricles of the cerebral hemispheres and with the cavities of the primitive optic vesicles. This neuromere possesses no motor nerves (Johnston, 1905), although their former existence may be suggested by the presence within it of the thalamic nucleus of origin of the somatic motor fasciculus. Warren (1911) asserted that in *Lacerta* and *Chrysemys* the commissura posterior is developed in this neuromere, and that its ultimate invasion of the mid-brain is due to secondary extension in caudal direction, and this has now been found to be the case in *Sphenodon* and the Chick.

Dendy (1910) has already shown that Johnston (1905) was wrong in assigning only the first epiphysis or pineal eye to this neuromere and referring the second epiphysis or pineal sac to neuromere IV: and the present investigation confirms Dendy's statement that the pineal outgrowths are paired dorsal structures belonging to this neuromere, while the recessus geniculorum are not, as Dendy supposed, lateral diverticula of the cavity of the mid-brain, but must also be referred to this neuromere. The pineal organs may be regarded as degenerated sense organs, the nervi pineales being special sensory nerves serially homologous with the optic nerves, and being connected centrally with the commissura superior, the habenular ganglia, and possibly with the commissura posterior.

In conclusion I wish to express my gratitude to Professor Dendy, in whose laboratory I have worked, for his invaluable advice and criticism during the progress of this research, and to Mr. C. Biddolph, of the Zoological Department of King's College, for his great kindness in preparing the series of excellent photographs of my models which have been used in illustrating this paper.

7. SUMMARY.

The brain of *Sphenodon* possesses a number of metamerically homologous paired diverticula of its central cavity (Dendy, 1910), which are found to afford valuable evidence as to the neuromeric segmentation of the fore-brain and the mid-brain.

(1) These paired diverticula have now been found to be arranged in two series, and not in a single series as suggested by Dendy.

(2) One of these series is dorsal and the other lateral, their positions being defined relative to the sulcus limitans, which is regarded as delimiting the dorso-lateral and latero ventral zones of the brain-wall.

(3) There is also a series of unpaired and somewhat less conspicuous medio-ventral diverticula.

(4) All of these diverticula appear nearly simultaneously and early in development. They first undergo considerable increase of size, which is occasionally followed by some reduction, but even in these instances considerable vestiges of the diverticula persist in the adult.

(5) The series of paired dorsal diverticula comprises the lateral ventricles of the cerebral hemispheres, the recessus optici laterales or small persistent vestiges of the cavities of the primitive optic vesicles, and the cavities of the pineal outgrowths.

(6) The series of paired lateral diverticula comprises the recessus preoptici laterales, the recessus thalami prænucleares, and the recessus geniculorum.

(7) The series of unpaired ventral diverticula comprises the recessus preopticus medius, the recessus postopticus or primitive infundibulum, and the recessus post-tuberculum.

(8) Series of recesses identical in position to, but generally of smaller size than, those mentioned above have now been demonstrated in the fore-brain of the Chick, Sparrow, and Gecko. Recesses apparently homologous with some of the members of these series have been figured in *Lacerta* and *Chrysemys* by Warren (1911) and in *Chelydra* by Johnston (1913).

(9) From the time of its first appearance as a shallow, laterally-elongated dilatation of the rostral region of the open neural groove the single primary fore-brain neuromere or prosencephalon of *Sphenodon* exhibits traces of segmentation into two 'secondary' neuromeres, and a third is faintly indicated. It is certainly present during the immediately subsequent stage of development.

These neuromeres are the short rostral Primary Telencephalon, the larger Diencephalon, and the smaller caudal Synencephalon.

(10) It appears that the brain of *Sphenodon* never passes through a true three-vesicle stage of development, although this condition is to some extent simulated for a very short time

during some of the earliest stages of development, owing to the indistinct external demarcation of the neuromeres, but even during this period the internal inter-neuromeric boundaries are clearly distinguishable.

(11) Each of the fore-brain neuromeres contains one dorsal pair, one lateral pair, and one of the ventral unpaired diverticula, described above.

(12) The cavity of the primary telencephalon is much reduced, a vestige of its proof persists as the tela choroidea or ependymal fold lying between the hemispheres of the secondary telencephalon (cerebral hemispheres), the lateral ventricles of the latter being the paired dorsal diverticula of the central cavity of this neuromere, of which the recessus preoptici laterales are the paired lateral diverticula, and the recessus preopticus medius is the unpaired ventral diverticulum.

(13) The cavity of the diencephalon possesses a pair of dorsal diverticula, the cavities of the pineal outgrowths, a pair of lateral diverticula, the recessus optici laterales, and an unpaired ventral diverticulum, the recessus postopticus.

(14) The cavity of the synencephalon possesses a pair of dorsal diverticula, the cavities of the pineal outgrowths, a lateral pair, the recessus geniculorum, and a ventral diverticulum, the recessus post-tuberculum.

(15) The mid-brain has now been shown to contain two, and the hind-brain seven, definitive neuromeres. The consideration of these is deferred to a later paper.

(16) The hind-brain is the dominant feature during the earlier stages of development, and is the first of the brain segments to develop a complete roof. During the same period the mid-brain is more conspicuous than the fore-brain, the latter remaining open by means of a longitudinal neuroporic slit for a considerable time after the roof of the mid-brain is complete.

(17) The primitive optic vesicles are at first inconspicuous, but they develop rapidly and become the most prominent feature of the fore-brain before the closure of the neuropore is complete.

(18) The account of the development of the paraphysis and of the pineal outgrowths given by Dendy (1910) has been confirmed, as has also the presence of the chief fore-brain nerve-tracts and nuclei described by Hines (1923).

(19) The three neuromeres of the fore-brain of *Sphenodon* must be regarded as definitive neuromeres, morphologically equivalent to those of the mid-brain and hind-brain, since they appear as early as do the neuromeres of these, and because they are not merely dorsal structures but contain also lateral and ventral components.

(20) In the Chick the number, topography, and general morphology of the fore-brain, mid-brain, and hind-brain neuromeres appear to be the same as in *Sphenodon*.

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EXPLANATION OF THE PLATES.

PLATE I.

Fig. 1. *Sphenodon*, Stage D. Embryo 58.   Dorsal view (× 100).
    2.   „   Stage E,   „   56.   Left side of brain (Model × 100 reduced to × 50).
    3.   „   „   „   „   Dorsal view (Model ×100 reduced to × 50).
    4.   „   „   „   „   Dorsal view of head, Dendy, 1899, fig. 21.
    5.   „   Stage F,   „   61.   Left side of brain (Model × 50).

PLATE II.

Fig. 6. *Sphenodon*, Stage F, Embryo 61.   Medial view of left half of brain (Model × 50).
    7.   „   Stage G,   „   59.   Left side of brain (Model × 50).
    8.   „   „   „   „   Dorsal view of brain (Model × 50).

PLATE III.

Fig. 9. *Sphenodon*, Early Stage J. Embryo 44.   Left side of brain (Model × 50).
    10.   „   „   „   „   „   Inside of right half of brain (Model × 100).
    11.   „   „   „   „   „   Rostro-dorsal view of brain (Model × 50).
    12.   „   Late Stage J,   „   79.   Left side of brain (× 100 reduced to × 50).
    13.   „   „   „   „   „   Rostro-dorsal view of brain (Model × 100 reduced to × 50).
    14.   „   Stage K,   „   39.   Left side of brain (Model × 50 reduced to × 25).

PLATE IV.

Fig. 15. *Sphenodon*, Stage L, Embryo 50.   Left side of brain (Model × 50 reduced to × 25).
    16.   „   Stage N,   „   14a.   Left side of brain (× 20).
    17.   „   „   „   „   Left side of brain-cavity (× 20).
    18.   „   „   „   „   Transverse section through fore-brain (× 46).
    19.   „   Stage P,   „   45a.   Left side of brain (× 20).

PLATE V.

Fig. 20. *Sphenodon*. Stage P, Embryo 45a. Left side of brain-cavity (× 20).
21.   „   „   „   „   .. Horizontal section through brain.
22.   „   „ PQ. „   51a. Left side of brain (× 20).

PLATE VI.

Fig. 23. *Sphenodon*, Stage PQ, Embryo 51a. Left side of brain-cavity (× 20).
24.   .,   ,,   ,,   ,,   ., Transverse section through telence-
                                    phalon anterior to Lamina termi-
                                    nalis (× 40).
25.   .,   ,.   ,,   .,   „ Transverse section through telence-
                                    phalon and dorsal sac (× 40).
26.   ..   Stage Q,   „   52a. Left side of brain-cavity (× 20).

PLATE VII.

Fig. 27. *Sphenodon*, Stage R, Embryo 162.   Left side of brain (Model × 25 reduced
                                              to × 12½).
28.   .,   ,,   ,,   „ Left side of brain-cavity (Model × 25
                              reduced to × 10).
29.   .,   ,,   .,   „ Ventral view of brain-cavity (Model
                              × 25 reduced to × 10).
30.   .,   ,.   ,. 111. Transverse section through telence-
                              phalon anterior to Lamina termi-
                              nalis (× 30).
31.   „   Adult No. I.   Transverse section through cerebral hemi-
                            spheres, recessus preopticus medius, and optic
                            chiasma (× 15).
32.   .,   ,.   .,   Transverse section through fore-brain in region
                            of recessus thalami praenucleares (× 15).

PLATE VIII.

Fig. 33. Chick embryo, 72 hours. Left side of brain (Model × 50 reduced to × 25).
34.   .   .,   72 „   „ brain-cavity (Model × 50 reduced to
                                  × 25).
35.   ..   ..   96 „   ., brain (× 20).
36.   .,   .,   96 „   .. brain-cavity (× 20).

PLATE IX.

Fig. 37. Chick embryo, 144 hours. Left side of brain (Model × 20 reduced to × 10).
38.   „   „ 144 ,.   „ brain-cavity (Model × 20 reduced to
                                  × 10).
39.   „   ., 192 ..   „ brain (Model × 20 reduced to × 10).
40.   „   „ 192 „ Right side of brain-cavity (Model × 20 reduced
                          to × 9).
41.   „   „ 192 .. Ventral view of brain-cavity (Model × 20 reduced
                          to × 9).

Reference list of lettering of Figures.

a.i.p., anterior intestinal portal ; *aud.*, auditory pit or vesicle ; *ang.vent.*, angulus
ventralis ; *b.M.*, bundle of Meynert ; *b.olf.*, bulbus olfactorius ; *c.a.*, commissura
anterior ; *c.hip.*, commissura hippocampi ; *cbl.*, cerebellum ; *c.c.*, cortical cells ; *C.H.*,
cerebral hemisphere ; *ch.pl.l.v.*, choroid plexus of lateral ventricle ; *Di.*, dience-
phalon ; *d.s.*, dorsal sac ; *D.T.g.*, di-telencephalic groove ; *ep.*, epiphysis ; *f.M.*,
foramen of Monro ; *for.int.*, foramen interventriculare ; *f.v.n.*, formatio vomero-
nasalis ; *g.pall.*, general pallium ; *H.B.*, hind-brain ; *Ha., Hb., Hc., etc.*, primary

segments of hind-brain; *hip.*, hippocampus : *H.ot.N.*, otic neuromere; *hyp.*, hypophysis; *hypopal.*, hypopallium ; *H.ep.*, head epiblast; *H.C.m..c.*, canal of mandibular head-cavity ; *inf.2*, caudal extension of intundibulum, *i. e.* definitive infundibulum ; *isth.*, isthmus ; *it.*, iter ; *l.v.C.H.*, lateral ventricle of cerebral hemisphere ; *l.f.b.*, lateral fore-brain tract ; *l.t.*, lamina terminalis ; *l.s.n.*, lamina supra-neuroporica ; *m.f.b.*, medial fore-brain tract ; *M.B.*, mid-brain : *M.B.1.*, *M.B.2.*, 1st and 2nd mid-brain neuromeres; *n.olf.*, nervus olfactorius; *ntc.*, notochord ; *nuc.c.ab.*, nucleus commissuræ aberrantis; *n.g.*, neural groove; *np.*, neuropore; *np.sl.*, neuroporic slit ; *N.g.2*, neuromeric groove of diencephalon; *n.1*, *n.2*, *etc.*, cranial nerves, *N.*, neuromere ; *nuc.ac.K.*, nucleus accumbens of Kappers; *nuc.l s.*, nucleus lateralis septi ; *n.m.s.*, nucleus medianus septi ; *nuc.olf.l.*, nucleus olfactorius lateralis ; *nuc. preop.*, nucleus preopticus ; *nuc.perie*, nucleus periventricularis : *nuc.v.m.*, nucleus ventro-medialis; *o.ch.*, optic chiasma or its rudiment ; *olf.ped.*, olfactory peduncle , *o.n.*, optic nerve; *o.st.*, optic stalk ; *o.v.*, optic vesicle or its rudiment ; *o.s.*, oral sinus ; *ot.N.*, otic neuromere ; *par.*, paraphysis or its rudiment , *par.p.*, paraphysial pouch ; *p.e.*, pineal eye or its rudiment ; *ps.*, pineal sac ; *p.stk.*, pineal stalk ; *p.d.t.*, pars dorsalis thalami ; *p.v.t.*, pars ventralis thalami ; *pr.f.g.*, primitive fore-gut , *phx.*, pharynx ; *pyr.l.*, pyriform lobe; *r.g.*, recessus geniculi ; *r.o.l.*, recessus optici lateralis ; *r.post.o.*, recessus postopticus ; *r.pre.o.l.*, recessus preopticus lateralis , *r.pre.o.m.*, recessus preopticus medius ; *r.t p.*, recessus thalami prænuclearis ; *s 1, s.2*, somites 1 & 2 ; *sd.*, sulcus dorsalis ; *s.l.*, sulcus limitans ; *s.m.*, sulcus medius ; *s.v.*, sulcus ventralis ; *s.intt.*, sulcus interstriatilis ; *s.sst*, sulcus superstriatilis ; *s.end.*, saccus endolymphaticus ; *Sy.*, synencephalon ; *Sy.M.g.*, syn-mesencephalic groove *T₁T₂*, primary and secondary telencephalon ; *T₁r.p.*, roof-plate of primary telencephalon ; *tel.ch.*, tela choroidea ; *Thal.*, thalamus ; *t.ht.*, tractus hypothalamicus ; *t.olf.*, tractus olfactorius ; *t p.*, tractus pinealis ; *t.tb.*, tractus tecto-bulbaris , *t.ts.*, tractus thalamo-striatilis ; *tub.olf.*, tuberculum olfactorium ; *v t*, velum transversum ; *V.P.₁*, *V.P.₂*, *etc.*, visceral pouches 1, 2, etc.

11. The Larval Development of some British Prawns (*Palæmonidæ*). II. *Leander longirostris* and *Leander squilla*. By Robert Gurney, M.A., F.Z.S.

(Text-figures 1–12.)

Having dealt in some detail with the development of *Palæmonetes varians* (Gurney, 1924), it was my intention to describe also that of the remaining British species and to compare these Palæmonidæ as a whole with other Caridea; but the appearance of M. Sollaud's work on the larvæ of Palæmoninæ (1923), in which a full account is given of the larval stages of *L. serratus* among others, and his promise (p. 513) of a further paper dealing with the bearing of his work on the comparative morphology of the Caridea, have rendered part of my programme unnecessary. On the other hand, the development of *L. longirostris* is entirely undescribed and that of *L. squilla* only partially known, and it may therefore be worth while to give some account of these two species.

In my account of *P. varians* I distinguished five main stages and showed that, while development might be completed within four moults, five were frequently passed through and, in captivity, the course of development was so changed that definite stages could scarcely be recognised. In the case of *L. longirostris* and *L. squilla* I have not been able to obtain sufficient material to follow the whole series of moults, but the evidence is consistent with the supposition that there are five stages only. Mortensen (1897) found only five stages in *L. adspersus* (= *L. fabricii*), while I have satisfied myself that five are usual in *L. serratus*, though a sixth may sometimes be added. For my material of the younger stages of this species I am indebted to Miss Lebour and to Mr. A. J. Smith, of the Plymouth Laboratory, while I have picked out a number of older larvæ from plankton samples taken in the English Channel and stored in the laboratory. The identification of these specimens is made certain by the season of their capture—not later than May (see Gurney, 1923, p. 101).

M. Sollaud appears to have worked mainly on larvæ kept through several moults in the laboratory, and my own experience with *P. varians* leads to the conclusion that the course of development is so profoundly affected by captivity that the changes observed cannot be taken as typical for larvæ under natural conditions. M. Sollaud himself states (p. 542) that he has only taken "Mysis" stages in the plankton, and that these almost always transform to the post-larval stage in one moult. It seems therefore that, after stage III, the series of stages

described by him (IV to VIII) are somewhat abnormal, corresponding with the intermediate stages found in *P. varians* in cultural conditions. If this is so the course of development is precisely the same in all species, namely five distinct stages, the last of which may sometimes persist over a second moult, so that stage V may be subdivided into stages V A and V B. Daday (1907) states, in the case of *Caridina wyckii*, that changes take place between stages without a moult, but of this I have seen no evidence in any Decapod larva.

M. Sollaud has pointed out an error in Miss Webb's note (1921) of the structure of stage III, and she is certainly wrong in stating that there are only four distinct larval stages.

The question of the number of stages is of some importance in comparison with other Caridea, and should be precisely established when possible. Miss Webb has distinguished (1921, p. 390) nine stages in the development of *Alpheus ruber*, but allows only four to *Pandalus* and *Crangon*, whereas in the former there are certainly eight and in the latter five.

LEANDER LONGIROSTRIS M. Edwards.

The adults are quite easily kept alive either in fresh or in salt water without any special precautions as regards circulation or aeration of water, but the eggs will not, so far as my experience goes, hatch in fresh water. The eggs hatch most readily and the larvæ thrive best in pure sea-water. One female was kept for two years in fresh water, and in the summer following capture produced eggs, but these did not become fastened to the pleopods, and it is doubtful if they were fertilised. I have still a number of adults which have lived in fresh water since July 1922, but I have not found any of them with eggs.

The development of the larva certainly takes place at sea, and it is probable that the majority do not return until after the post-larval stage is reached. Even late larvæ are very rare in the estuary of Breydon Water, and I have only twice taken single specimens of stage I. The larvæ of *L. squilla* are also not found as a rule in in-shore waters, and those of *L. serratus* are very rare. It is of special interest to note that a larva in stage V which unquestionably belongs to *L. longirostris* was taken in the young-fish trawl at Plymouth in July 1922. These larvæ must therefore be distributed far and wide, and it is difficult to understand how it is possible for races of restricted distribution to become established, as appears to be the case with *L. longirostris* and *L. squilla* (De Man, 1915 and 1923).

Larvæ of *L. longirostris* hatched in the laboratory have been kept alive for about 14 days, during which time the few survivors had passed through two moults. I am therefore able to give an account of stages I-III from laboratory material. As the effect of cultural conditions does not make itself felt in *P. varians* until after this stage, I have no doubt that these larvæ were perfectly normal except in size.

It would probably be quite possible to rear these larvæ through all stages, but it has been impossible for me to supply them with the necessary food and changes of water.   In the absence of Entomostraca the larvæ devour each other, and the numerous mangled bodies which fall to the bottom contributed by their decay to my failure to keep the survivors beyond the second moult.

Hatching takes place at night, and the larval cuticle is thrown off in the egg, not by a process of complete moult, but having apparently been torn to shreds by the growth of the setæ of the telson and limbs.

The larvæ are strongly attracted by light, the majority collecting at the sides of the aquarium facing the strongest light, where they rest head down with the back to the glass and the exopodites constantly moving and causing a whirl of water from behind forwards and inwards to the mouth.

Text-figure 1.
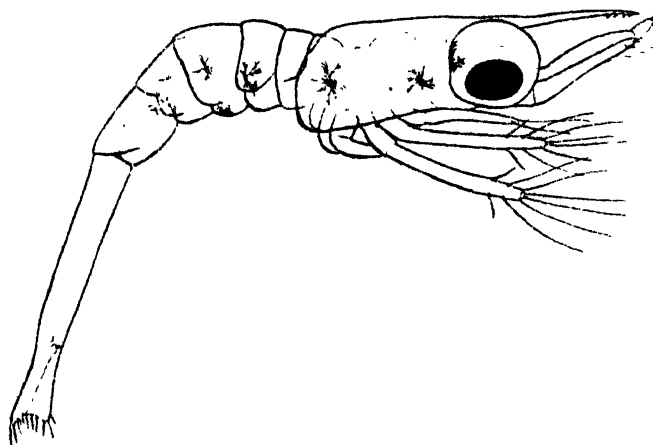
Leander longirostris.
Stage I.

STAGE 1.   (Text-fig. 1.)

Length 3·3–3·5 mm. (from extremity of rostrum).

Colour.

The larvæ appear golden yellow by reflected light, but of an orange colour by transmitted light under the microscope.   The pigment is localised in chromatophores which are constant in position, and are shown in the accompanying figures.   The majority of these chromatophores have a yellow centre and red branches, but a few, such as the pair on the 5th abdominal

somite, are red only. The black pigment of the eye is largely masked, in reflected light, by yellow surface pigment which is not seen in transmitted light.

Structure.

A detailed account of the structure is unnecessary since the form of the appendages is practically identical in all species. Admirable figures have been published by Mortensen (1897) for

Text-figure 2.
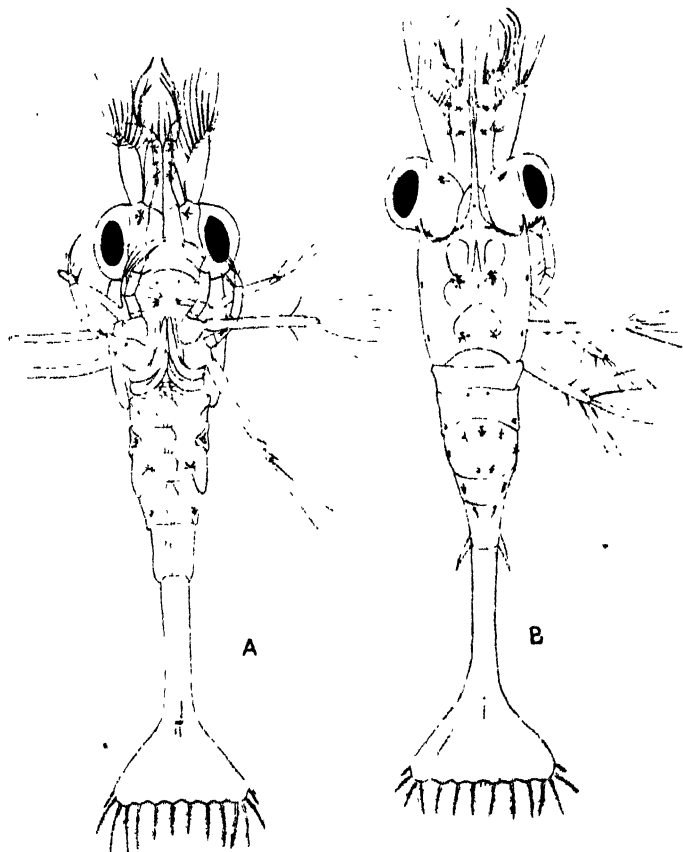
Leander longirostris.

A. Stage I.   Ventral view.   B. Stage II. Dorsal view.

L. adspersus, and M. Sollaud's paper (1923) deals in detail with the appendages of *L. serratus*. The following summary of the characters of this and later stages should suffice for comparison with other species.

Rostrum slender, slightly down-curved and armed at the end with a few minute hooks. As a rule projecting slightly beyond the 1st antenna.

Abdominal somites entirely without spines or processes. Telson exactly as in *L. serratus*. The embryonic cuticle, if examined some time before hatching, is found to bear only six spines on each side, the innermost enclosing two of the larval spines. The embryonic formula is therefore 6+6, as it is also in *L. squilla* and such other Caridea as I have been able to examine.

Appendages precisely as in *L. serratus* with the exception that rudiments of all five pairs of pereiopods are visible, those of legs 1 and 2 being large and biramous, while legs 3-5 are represented by minute buds. In *L. serratus* and *L. squilla* there is no trace of these legs.

Text-figure 3.
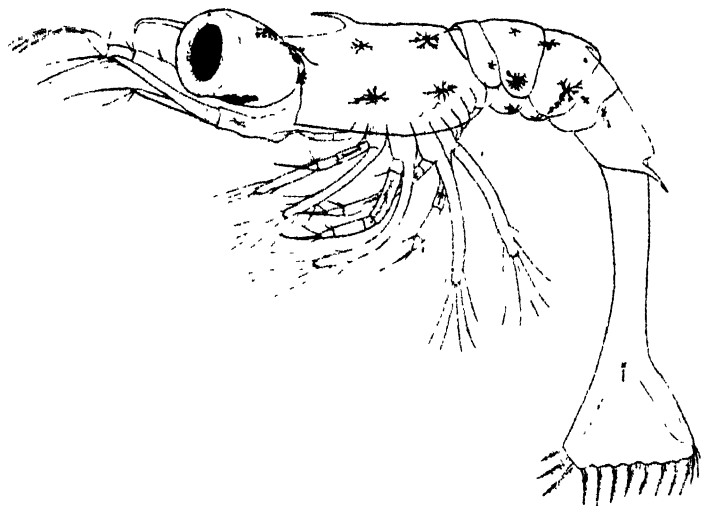
Leander longirostris.

Stage II.

STAGE II. (Text-fig. 3.)

Larvæ kept in an aquarium moulted on the seventh day after hatching into the 2nd stage. It is curious that the only specimen of this stage that I have seen other than those reared in the laboratory was picked out from among the abdominal appendages of a female which had recently hatched her young but had not yet moulted. This larva had evidently remained entangled here for some days, and provides evidence that the moulting of the adult does not occur immediately after hatching, as is commonly

the case among Decapods. The parent of the larvæ hatched in my aquarium moulted ten days later, and a large female which, to judge from the condition of its pleopods, had just hatched a brood, did not moult till the 33rd day !

Length about 3·5 mm.*

Colour.

The general coloration remains the same, though a larger number of chromatophores are present and some blue pigment appears in a transverse line across the carapace behind the eye, and in the eye itself. In transmitted light the general colour is pink or orange, while in reflected light it is light yellow, particularly on the eyes and a line across the thorax behind the eyes. The chromatophores are dichroic, with an opaque yellow and a transparent red pigment.

Structure.

Rostrum no longer toothed, but abruptly down-curved at the end into a small hook.

Carapace with one median and a pair of supraorbital toothed spines.

Fifth abdominal somite with a pair of dorso-lateral spines. Legs 1 and 2 developed, with 5-jointed endopodites and setiferous exopodites. Legs 3–5 rudimentary, the rudiment of leg 5 considerably the largest.

Rudiments of gills present above legs 1 and 2. These gills are so close to the attachment of the legs that they really occupy the position of arthrobranchs.

STAGE III. (Text-figs. 4, 5.)

Of a brood hatched on July 22 a few survivors were found on August 3 to be in stage III. All were dead on the following day.

Length 3·5 mm.

Colour.

The colouring of the animal has changed to some extent by the appearance of blue pigment on the antennæ and eyes, and the red pigment in the thorax seems to preponderate over the yellow. In these respects some approach has been made to the adult colouring.

Structure.

Rostrum without terminal hook.

Carapace with an additional median spine.

Telson separated from 6th abdominal somite and more elongated. Outermost spine very small and situated somewhat on the outer edge.

* The measurements for stages II and III are probably abnormally small.

Uropods developed, the endopodite very small and without setæ. Legs 1 and 2 as before. Legs 3 and 4 still rudimentary, but larger. Leg 5 fully developed into a long, uniramous, jointed appendage with terminal spine and bent forwards under the thorax, nearly reaching the mouth.

Text-figure 4.
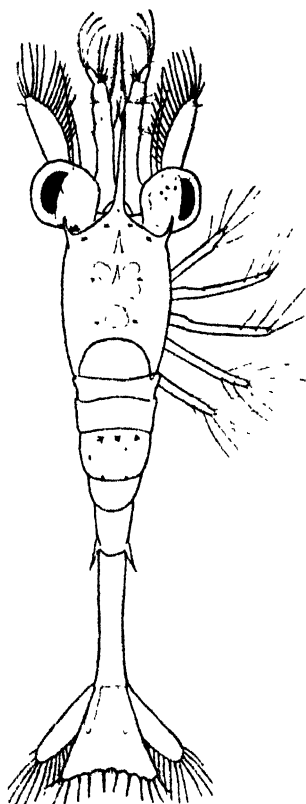
Leander longirostris.

Stage III.

In respect of the precocious development of this appendage, *L. longirostris* differs at this stage strikingly from *L. serratus* and *L. adspersus* and approaches *P. rarians*, but in the latter the 3rd leg is developed in stage III.

The five pairs of pleurobranchs are visible, those of the last pair being largest and those of legs 3 and 4 minute. In

L. serratus the gill of leg 5 is smaller than those of legs 1 and 2 (Solland).

Pleopods appear on somites 2 to 4 in the form of minute buds.

Text-figure 5.
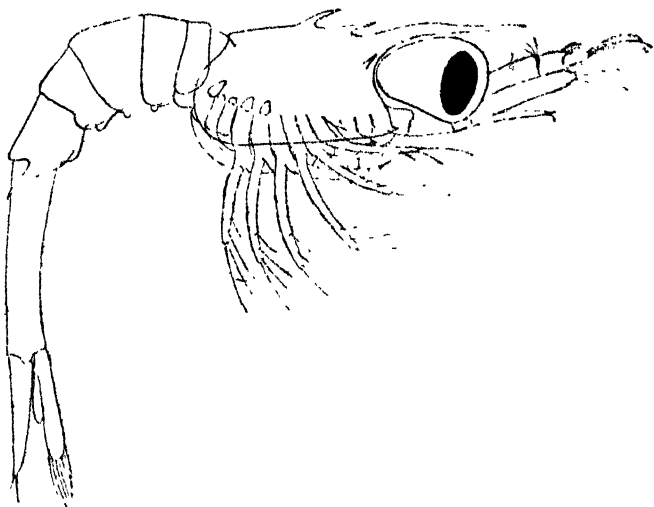
Leander longirostris.
Stage III.

STAGE IV.

No specimens corresponding to stage IV of *P. varians* or *L. adspersus* have been seen, but must certainly occur.

STAGE V. (Text-fig. 6.)

A few specimens of this stage were caught in the tow-net on Breydon Water in August, but, though larvæ of other Decapods which do not occur as adults in Breydon (e. g. *Porcellana*) were taken in some numbers, the larvæ of *L. longirostris* were extremely rare. On two occasions I have been out with a shrimper as far as the Cockle Light off Yarmouth, and have failed to get any *Leander* larvæ. One specimen of this stage was taken at Plymouth on July 10, 1922.

Length 7·5 mm.

Colour.

These larvæ appear colourless and transparent to the naked eye, but actually have a number of small chromatophores. The eyes are tinged with pink on the outer edge, and have a large red and yellow chromatophore on the posterior side. The pigment of the retina appears greenish yellow in reflected light but black in transmitted light.

Text-figure 6.
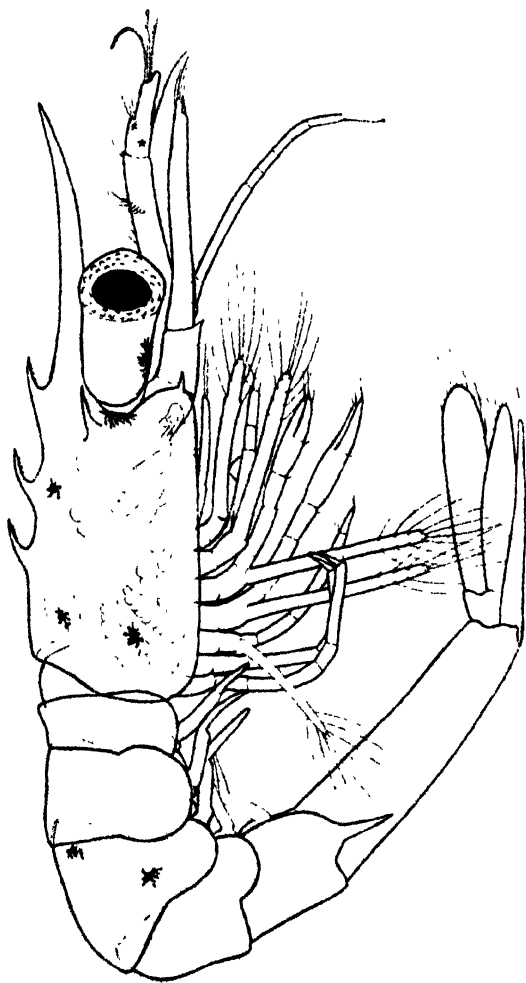
Leander longirostris. Stage V.

Behind the eye is a transverse line of dark red and purple pigment. On the thorax only three pairs of very small chromatophores were seen, two dorsal and one lateral.

There is a pair of small red chromatophores dorsally on the second abdominal somite and three dark-coloured spots on the anterior margin of the third somite, besides a lateral pair. Between the uropods is a small orange-red chromatophore. The basipodites of each of the thoracic appendages except the 1st maxillipedes are faintly tinged with yellow, and there is a large yellow chromatophore at the base of the 3rd pleopods: otherwise the limbs are colourless.

Structure.

Rostrum about as long as antennal scales, sabre-shaped, upcurved.

Carapace with three median toothed spines, supraorbital spines, and pterygostomial spines.

The somites of the abdomen approach the form of the adult, the pleura of the 2nd overlapping slightly somites 1 and 3. Fifth somite with long posterior spinous processes. Telson narrow, parallel-sided, with only 8 terminal spines and no lateral spines. It is evident that the lateral spines of the adult are new acquisitions not represented in the larva.

There is no ventral terminal spine on the 6th somite such as there is in *L. squilla.*

All legs developed and functional, legs 1 and 2 being chelate. The chelæ are of relatively very great size, and the proportional length of the joints of these appendages differs greatly from that of the adult (see Table I.). The 5th leg is not notably larger than legs 3 and 4, and leg 4 has no exopodite. In this respect the larva of *L. longirostris* differs from that of *P. varians* and all other Leanders known. I have had four specimens for examination and in all cases the exopodite was absent, so that its absence cannot be regarded as abnormal.

Pleurobranchs of the pereiopods all developed, with lobed margins, but no other gills present.

First Post-larval Stage.

I have had only two specimens of this stage for examination, both of which were obtained by keeping the larvæ until the moult. One of these specimens was kept alive in the hope of following subsequent changes, but it died in the act of moulting 14 days later.

With the moult of the 5th larval stage the adult form is assumed in general structure, but there are still many differences in detail, some of which should be mentioned.

(1) Rostrum. The rostrum has the narrow form which is characteristic of the adult of *P. varians*, but it differs from that of *P. varians* of the same stage both in form and length, reaching quite to the end of the antennal scales, whereas that of

Palæmonetes falls considerably short of that point.   The proximal spine is situated just behind the ocular notch, whereas in the adult there are two spines on the carapace.   It seems that the three median spines of the larval carapace are lost, and it is also doubtful if the antennal spine of the adult is represented in the larva.

(2) 1st Antenna. The peduncle, while now of the adult form, differs in the proportional length of the joints and lacks the distal outer expansion of the 1st joint so characteristic of the adult.   The inner flagellum is scarcely longer than the 1st joint of the peduncle, and consists of only five joints.   The outer flagellum has a two-jointed basal part which bears a four-jointed outer flagellum and a one-jointed inner sensory part.

(3) The mandible still has no trace of a palp and has not assumed the deeply-cleft form of the adult.

(4) The exopodites of the 2nd and 3rd maxillipedes have lost their setæ.

(5) Pereiopods. The first three pairs retain reduced exopodites without setæ.   The proportional length of the joints in the first two pairs differs from that of the adult (see Table I.).

(6) Gills. There are six pairs of pleurobranchs, but the arthrobranch of the 3rd maxillipede and the podobranch of the 2nd are not developed.

Second Post-larval Stage.

A single individual of this stage was taken in the River Bure, seven miles above Yarmouth, quite by chance when washing some Cordylophora, after long-continued efforts to catch them by other means.

This specimen measured only 7·8 mm., showing practically no increase in size from the last larval stage.   It was profusely covered with small chromatophores, a few of which were pure red, but most of them orange-yellow with red branches.

The rostrum is still very narrow, with a formula of $\frac{7}{3}$; only one spine being behind the eye.

The changes in the 1st antenna and 2nd leg are shown in the following tables (p. 973).

Post-larval Growth.

I have dealt with the post-larval changes in *P. varians*, of which I had abundant material, but in the case of *L. longirostris* the material is quite insufficient for generalization.   At the same time, it is clear that the changes in the form of the 1st antenna and 2nd leg are of the same nature as obtain in *P. varians*, namely a gradual growth of the accessory flagellum in the former, which is probably not completed till near maturity, and a radical change in the proportions of the joints in the leg.

L. longirostris in stage V is characterised by the relatively enormous length of the dactylus of the 2nd leg, and indeed, unless the specimens examined are abnormal, which is unlikely, the species can be easily recognised by this character alone.

Text-figure 7.
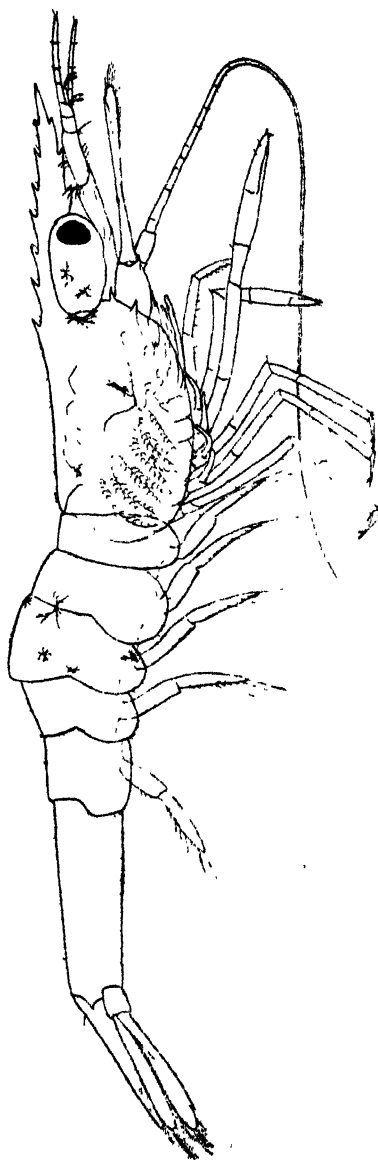
Leander longirostris.   First post-larval stage.

These changes, and the relative length of the joints, are shown in the accompanying tables.

TABLE I.

Leander longirostris. Table of measurements of 2nd Leg and outer flagellum of 1st Antenna, reduced to percentages of chela and peduncle respectively.

	Length.	2ND PEREIOPOD.					1ST ANTENNA.			
		Dactylus.	Chela.	Palm.	Carpus.	Merus.	Peduncle.	Flagellum.	Basal part.	Accessory flagellum.
3rd Larva	3·5 mm.	50	100	50	41	87	100	17	--	---
Last Larva	7·5 „	58	100	42	24	39	100	26	--	—
1st Post-larval	7·4 „	53	100	47	37	62	100	36	21	15
Young ♀	19 „	43	100	57	92	96	100	00	29	31
„ ♂	22 „	48	100	52	79	82	100	72	30	42
„ ♀	25 „	49	100	51	77	66	100	68	34	34
Adult ♀	50 „	38	100	62	124	124				
„ ♂	57 „	42	100	58	87	87				
„ ♀	75 „	42	100	58	89	91				
„ ♀	77 „	41	100	59	84	87				
„ ♂	69 „						100	64	17·5	46

TABLE II.

Measurements of the 2nd leg of the last larval stage, expressed as percentages of the length of the dactylus.

|		Dactylus.	Chela.	Palm.	Carpus.
P. varians.	Stage V.A	100	187	87	78
„	V.B	„	223	123	72
L. longirostris.	V.B	„	160	60	43
„	Plymouth	„	162	62	40·6
L. squilla.	V.B	„	191	91	74
L. serratus.	V.A	„	183	83	63
„	V.B	„	179	70	74
L. adspersus (Mortensen, pl. iii. fig. 3)		„	222	123	80

LEANDER SQUILLA.

A short description of the first larva of *L. squilla*, without
figures, has been given by Stuxberg (1874), and Keeble and
Gamble (1914) have described very carefully the distribution of
the chromatophores in the first stage. Miss Webb (1921) gives
a note of the size and colour of this same stage.

Just as was the case with *L. longirostris*, no early larvæ of
L. squilla have been found in plankton. A brood of larvæ was,
however, hatched from a female taken at Thornham on Sept. 6,
at which time breeding had nearly ceased. The breeding season
appears to last from May to August as a rule.

The larva sheds the embryonic cuticle before hatching, but,
shortly before leaving the egg, the limbs and telson are to be
found enclosed in this cuticle. The telson is then provided with

Text-figure 8.
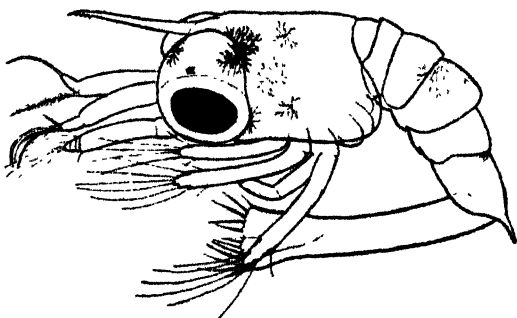
Leander squilla.

Stage I.

six large conical processes on each side, of which the five outer-
most enclose one of the future setæ. The innermost, on the
other hand, encloses two of these setæ.

Colour.

The difference in colouring between the larvæ of this species
and of *L. longirostris* is striking, since in the former nearly all
the colour is concentrated in the thoracic region, and the abdomen
appears quite colourless and inconspicuous. The distribution of
the chromatophores has been described in detail by Keeble and
Gamble, and they have traced a connection between those of the
larva and of the adult. I have not seen the two posterior
chromatophores on the carapace described by them, and should
point out that it is only in rather exceptional cases that three
distinct pigment spots can be seen on the 3rd abdominal somite.

Usually this somite appears to contain a single very much branched red chromatophore. It is only in the condition of extreme contraction that the three centres can be distinguished.

Text-figure 9.
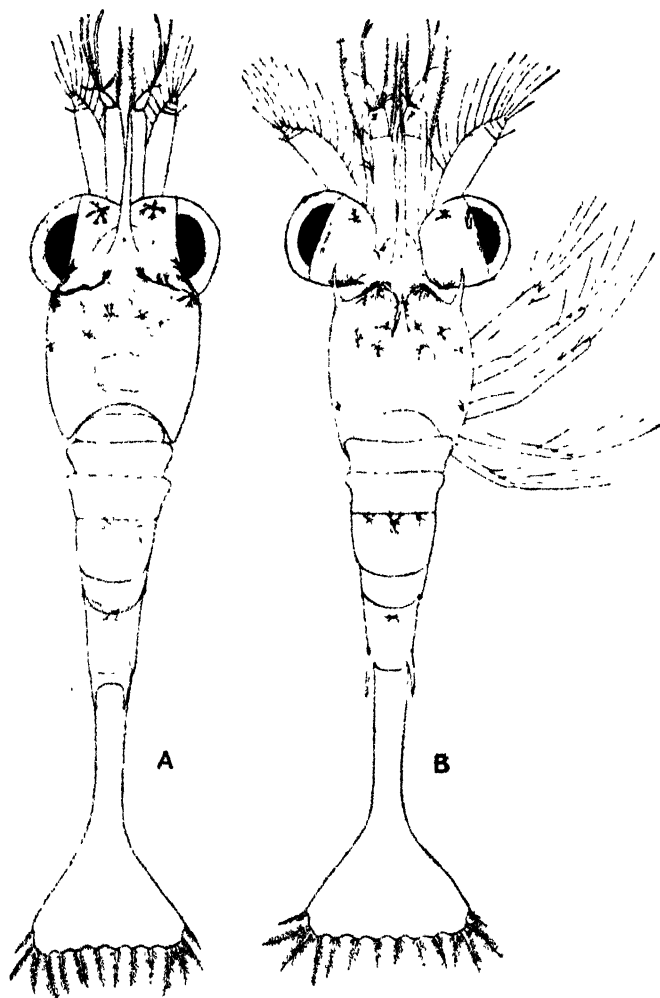
Leander squilla.

A. Stage I. Dorsal.   B. Stage II. Dorsal.

The general colour of the gastric region, in which most of the colour is concentrated, is orange-red due to mixture of red and opaque yellow chromatophores.

Structure.

Length 3·0–3·2 mm.

It is unnecessary to describe the structure of the larva which is practically identical in all respects with that of *L. longirostris* with the following exceptions. The posterior edge of the 5th abdominal somite is produced into a pair of small spines, whereas in *L. longirostris* and *L. serratus* these spines do not appear till the second stage. There is no trace of the pereiopods.

By its colour, size, and the presence of spines of the 5th abdominal somite the larva of *L. squilla* may easily be recognised in stage I.

STAGE II. (Text-fig. 10.)

Length 3·13–3·7 mm.

The larvæ moulted into the second stage in about a week, but all died before moulting a second time. Being away from home at the time, I am unable to give any notes as to the coloration at this stage. In structure the larva is, apart from its somewhat smaller size, indistinguishable from that of *L. longirostris*. Among the specimens examined, one was found in which three pairs of pereiopods were developed instead of two. Of the rudiments of the last pairs only the fifth lack an exopodite.

Text-figure 10.
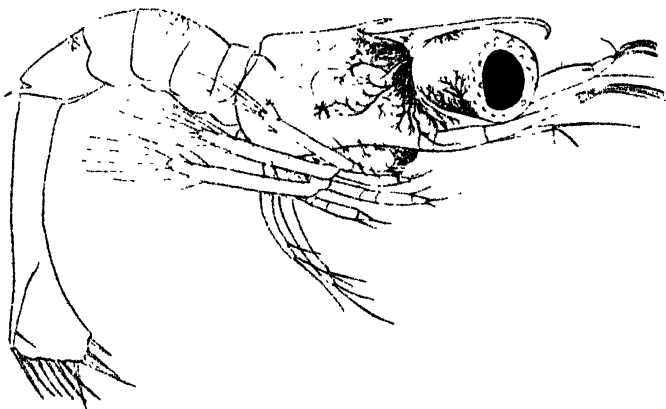
Leander squilla.
Stage II.

I have not succeeded in rearing the larvæ of *L. squilla* beyond stage II, and have altogether failed to obtain free larvæ in stages III and IV. As is apparently the case with *L. longirostris*, the whole larval life seems also to be spent in *L. squilla* in the open sea; but in this case the return to the shore is, I think, delayed as a rule until after the transformation to post-

larval. I have made several attempts to catch these larvæ in Wells Harbour, where the adults abound, but without success until this year, when, on July 20, I obtained one larva in the last stage after repeated hauls with a large tow-net.   Several early larvæ of *P. varians* were taken at the same time which had been washed out to sea by a very high tide.

In August very small specimens of *L. squilla*, 10 or 12 mm. long, may be taken in numbers in Wells Harbour, though I have only taken one or two which could be recognised as being in the 1st post-larval stage.   It seems probable that the transformation and also the 1st post-larval moult take place as a rule at sea, and that the young prawns then find their way in-shore.

STAGE V (moulted skin).   (Text-fig. 11.)

Length of rostrum and thorax .....   2·93 mm.
   ,,   abdomen ....   4·93 ,,

Total ....   7·86 mm. (approximate).

In life the animal appeared almost colourless with only a slight pinkish tinge in the thorax, but it was not examined under the microscope.

Text-figure 11.
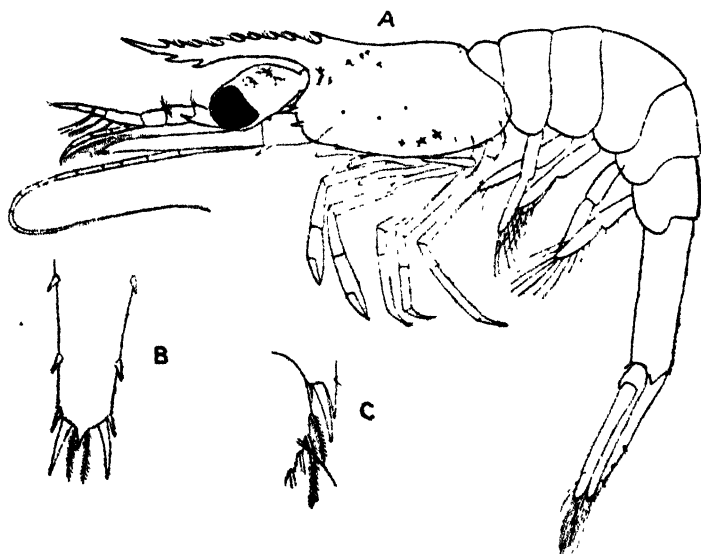
Leander squilla.   Stage V.

A. Lateral view.   B. Telson.   C. Outer angle of uropod (exopodite).

In general form and in the structure of the appendages I can find no appreciable differences from the larva of *L. serratus* or *L. adspersus*.   The following points only need be mentioned :—

(1) The pleura of the abdominal somites approach, as has been said in the case of *L. longirostris*, the form of the adult. Somite 1 has an anterior prolongation or accessory tergite which is hinged upon the somite and passes under the carapace. The main tergite overlaps somite 2, while its pleuron is overlapped by it. The pleuron of somite 2 is therefore overlapped a little by somites 1 and 3.

(2) At the posterior end of the 6th somite there is a small median ventral or "preanal" spine. There is no such spine in *L. longirostris* or *P. varians*, and it is difficult to be sure from Mortensen's figures whether it is present or not in *L. adspersus*.

. Text-figure 12.
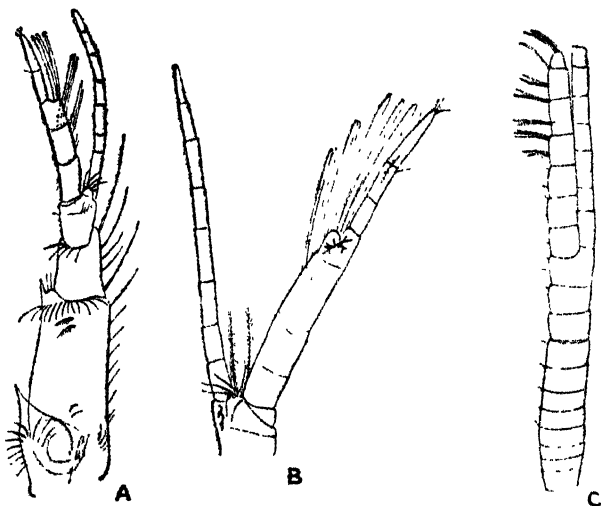
Leander squilla. First antenna.

A. Moulted skin of second post-larval stage.
B. Flagella of stage arising from this moult, showing first trace of accessory flagellum.
C. Outer flagellum of young specimen 26 mm. long.

A similar spine is found in all the larvæ in stage V taken at Plymouth and referred to *L. serratus.* It is not mentioned by Sollaud, but it is possible that in this small point there may be a means of distinguishing at least *L. squilla* and *L. serratus* from the other species.

First Post-larval Stage.

Of this stage I have examined three specimens, one of which was derived by moult from the last larval stage. They measured 8·5–8·62 mm.

The moulted specimen appeared in life to be nearly colourless, with only a little red pigment in the thorax, as in the larva.

The rostrum is very narrow, nearly straight, and does not reach the end of the antennal scale. It has 9 teeth above, of which only one is behind the eye, and 3 below, the foremost reduced to a minute point. The spine formula is therefore the same as in the adult. All the appendages have assumed nearly the adult form.

The 1st antenna has an inner ramus of five joints approximately of the same length as the outer branch, while the latter consists of three basal sensory joints and two slender distal joints, without any trace of an accessory flagellum. The pereiopods retain vestiges, without setæ, of the exopodites, and the proportional length of the joints in legs 1 and 2 differs greatly from that of the adult.

The pleura of the 5th abdominal somite are rounded, the spinous processes of the larva being lost. The 6th somite has a conspicuous "pre-anal" spine. This spine seems to be usually lost in the adult, though it is sometimes to be found reduced to a minute prickle. In *L. serratus* it is apparently always retained in individuals about half-grown (up to 55 mm.), but I have not found it in the adult. It is also not present in adults of *L. adspersus* and *L. longirostris*.

POST-LARVAL GROWTH.

Here again the 1st antenna only gradually attains to the adult form, and the proportional length of the joints in leg 2 changes considerably.

1st Antenna. The accessory flagellum does not begin to appear until the 2nd post-larval moult as a small knob, and in specimens of 12 mm. (probably about the 5th moult) it is still only of one joint, while the whole outer flagellum is about half the length of the peduncle.

In the adult of *L. squilla* var. *intermedia* De Man, of the Dutch and British coasts, the accessory flagellum is considerably longer than the basal or "fused" part, but it remains shorter even up to a length of about 30 mm. (see Table III.). Males are mature at a size of about 25 mm., and females may bear eggs when but little over 30 mm. In one sample of 56 specimens from Blakeney the size of egg-bearing females ranged from 44 to 31 mm., and in another of 78 from Wells the range of size was from 56 mm. down to 31 mm. It is mainly upon the relative length of the accessory flagellum as compared with the basal part of the flagellum that De Man (1915) founded his separation of the varieties of the species, and it is clear that reliance cannot be placed on the distinction unless the specimens are not only mature but of considerable size.

2nd Leg. In the last larval stage the dactylus is about half the length of the chela, and the carpus is even shorter than the

dactylus; whereas in the adult the chela is three times as long as the dactylus and the carpus nearly the same length as the chela. Chela and carpus grow in length rapidly, but do not attain the adult proportions till a size of over 30 mm. is reached, as is the case with the 1st antenna.

TABLE III.

L. squilla. Measurements of Leg 2 and Antenna 1, showing changes in post-larval growth.

| | Sex. | Length (mm.). | Leg 2. | | | | | Antenna 1. | | |
			Dactylus.	Chela.	Palm.	Carpus.	Merus.	Peduncle.	Basal part.	Accessory flagellum.
Larva, Stage V		7·86	100	196	96	68	—			
1st Post-larval		8·5	,,	266	166	166	—			
,, ,, ...		8·62	,,	229	129	132	150	100	34	—
2nd ,, ...		8·3	,,	207	107	136	151	,,	39	—
3rd (?) ,, ...		8·56	,,	211	111	150	177	,,	42	—
Young stage......	♀	12·6	,,	217	117	121	148	,,	38·5	18·5
,, ...	♀	13	,,	243	143	216	188	,,	—	—
,, ...	♀	14	,,	249	156	210	200	,,	51	19·5
·, ...	♂	15	,,	250	150	221	207	,,	51	21
,, ...	♀	16	,,	255	155	246	229	,,	48·4	17
,, ...	♂	18	,,	282	182	282	249	,,	48	24
,, ...	♀	20	,,	244	146	222	189	,,	52	17·7
Adult...	♂	24	,,	266	166	261	227	,,	46·5	33·3
,, ...	♀	31	,,	258	158	234	221	,,	—	—
,, ...	♀	33	,,	321	221	271	264	,,	49	39
,, ...	♀	59	,,	345	245	310	296	,,	46	61

COMPARISON OF THE LARVÆ.

In life the larvæ of all the British prawns are easily separated by colour alone, probably at all stages.

STAGE I.

(1) *P. varians.* General coloration yellow. A streak of yellow down centre of telson.

(2) *L. longirostris.* General coloration yellow. No chromatophores in 5th abdominal somite. Telson with small basal chromatophore, not forming median band.

(3) *L. serratus.* General coloration red, both in thorax and abdomen. Each abdominal somite with a large lateral chromatophore. Ventral chromatophores in at least the first three somites of abdomen.

(4) *L. squilla.* General coloration dark red, colour concentrated in mouth region, abdomen nearly colourless. The enormous development of the chromatophores in the maxillary region is characteristic of this species. (See p. 974.)

(5) *L. fabricii.* I have not seen this larva. From Mortensen's figures it appears to be of a faintly rosy colour, with a completely colourless abdomen.

Stage I.

Comparison of Structure.

(1) *P. varians.* Size 3·5–4 mm.
Rostrum shorter than peduncle of ant. 1.
All pereiopods present as rudiments.

(2) *L. longirostris.* Size 3·3–3·5 mm.
Rostrum reaching to or beyond end of ant. 1.
Legs 1 and 2 large rudiments; legs 3–5 traceable.

(3) *L. serratus.* Size 3·6–4 mm.
Rostrum usually shorter than peduncle of ant. 1, never quite as long as whole antenna. No trace of legs 3–5.

(4) *L. squilla.* Size 3·0–3·2 mm.
Rostrum reaches beyond peduncle of ant. 1, usually nearly to end of antenna. 5th somite of abdomen with a pair of small dorsal spines. No trace of legs 3–5.

(5) *L. adspersus* (Mortensen).
Rostrum much shorter than peduncle of ant. 1. No trace of legs 3–5 ?

In later stages the difficulty of separating the species is greatly increased, and it may be impossible to separate them. Size alone cannot be relied upon. I have not myself sufficient material to deal with these older stages, but it may be pointed out that *P. varians* and *L. longirostris* lack the pre-anal spine found in *L. serratus* and *L. squilla,* while *P. varians* is distinguishable by the order of appearance of the legs, and *L. longirostris* by the structure of the 2nd leg and absence of an exopodite from the 4th leg. Any larva taken off our coasts before June will almost certainly belong to *L. serratus.* (Gurney, 1923, p. 101.)

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42. The External Characters of the South American Edentates. By R. I. Pocock, F.R.S.

(Text-figures 14–37.)

Contents.

INTRODUCTION.

The observations recorded in this paper are based upon the examination of Armadillos of the genera *Euphractus* (formerly *Dasypus*) and *Dasypus* (formerly *Tatusia*), of Anteaters of the genera *Myrmecophaga* and *Tamandua*, and of Sloths of the genus *Bradypus* that died in the Zoological Society's Gardens while I was Superintendent. Of the two rare genera of Armadillos, *Tolypeutes* and *Chlamyphorus*, and of the rare Anteater *Cyclopes*, I have seen specimens preserved in alcohol in the Natural History Museum, which also contains similarly preserved material, mostly immature, of the other genera mentioned above, as well as a fine collection of dried skins, amongst which are examples of the Armadillos *Cabassous* (formerly *Xenurus*) and *Priodontes*, genera which I have not been able to examine in a soft state. Thanks, too, to the courtesy of Mr. R. H. Burne, I have been able to examine entire specimens and anatomical preparations of many of the commoner, and some of the rarer, genera of South American Edentates preserved in the Museum of the Royal College of Surgeons. It must be at once conceded that a very large number of the

facts recorded in the following pages have been known for
many years, and will be familiar to those who have studied this
order.   The literature relating to the Edentates, both from the
morphological and systematic standpoints, is so extensive that it
has been found impossible by bibliographical reference to do
justice to the claims of the numerous zoologists whose labours
have built up our knowledge of the structure and classification
of this order during the last hundred or more years.   My
omission to quote their names in the text that follows must not
be regarded as an indication of my failure to consult their
publications.   This paper, moreover, is not in any sense a com-
pilation from the works of previous authors.   It is based almost
wholly upon my own observations on all the available specimens
I could see ; and the justification for its issue lies in my belief that
no previous attempt has been made to deal with the genera of
Edentates on the lines adopted in this account of them.

One regrettable, but unavoidable, change in nomenclature will
puzzle those unfamiliar with recent systematic works.   This is the
transference of *Dasypus* from the Armadillos typified by *sex-
cinctus*, to the species formerly known as *Tatusia* or *Tatu* ; the
necessity for this was shown by Thomas in 1911.   The Arma-
dillos formerly known as *Dasypus*—i. e., *sexcinctus* and its allies
—take the name *Euphractus*.   These changes, however, were
adopted by Winge in his treatise on the Edentates in 1923.
My adoption of them therefore is not new.   Other changes less
momentous, but not quite so unfamiliar perhaps, are the substi-
tution of *Cyclopes* for *Cyclothurus* for the two-toed Anteater,
and of *Chlamyphorus* for *Chlamydophorus* for the aberrant Arma-
dillo long known under the latter name.

The Dermal Covering.

a. *The Hairs of the Anteaters and Sloths.*

In retaining the hairy coat, unaccompanied by dermal bony
scutes, the Anteaters and Sloths are less specialized than the
Armadillos.   In *Myrmecophaga* the hair is somewhat coarser
and longer than in *Tamandua*, and is especially well developed
on the tail, where it forms a long dorsal and ventral fringe.   In
Tamandua it is short and smooth almost everywhere.   In *Cyclopes*
(*Cycloturus*) it is thick and silky.   In the Sloth it is very coarse
and shaggy, but differs in texture in the genera, being de-
scribable as "pithy" in *Bradypus* and *Scæopus*, more normal in
Cholæpus.

b. *The Carapace of the Armadillos.*

In the Armadillos the integument is provided with bony scutes
covered with dermal scales, the hairs, which project through or
between the scutes, being usually reduced in numbers—at all
events, on the dorsal side.   In tolerably closely-related genera or
species, however, the hairy clothing varies considerably in extent

as in *Euphractus* and, more particularly, in *Dasypus*—where in one of the species, *pilosus*, the scutes are entirely covered beneath a thick coating of long hair, giving the animal the appearance of an ordinary mammal in this respect *. In most cases the hairs are comparatively coarse and scattered on the limbs as well as on the dorsal and ventral surfaces; but in *Chlamyphorus* the hairy clothing of the head and body, beneath the carapace, and of the limbs is short, close, and silky.

Since the dorsal armature has been frequently described, it is needless to devote much space to it here.

The carapace in typical Armadillos is divided into four distinct regions, the cephalic, scapular, dorsal, and pelvic shields, typically composed of transverse rows of scutes, those of the scapular and pelvic shield being immovably welded together, whereas more or fewer of the scutes of the dorsal area form jointed bands.

In the size, shape, and sculpture of the scutes there are frequently individual variations within the species and specific variations within the genera, but the general features of the armature are characteristic of the families or subfamilies whichever rank be assigned to them.

Starting with *Priodontes*, which has apparently the least differentiated carapace, we find that the scutes on the whole show a steady increase in size from the neck to the anterior part of the pelvic shield. Those of the free dorsal bands, of which there are about 13, are tolerably regularly oblong in shape, whereas those of the 16 or so fused pelvic bands and of the 10 composing the scapular shield are mostly more irregularly pentagonal or even hexagonal in outline, about four rows at the anterior end of the scapular shield forming free cervical bands.

Cabassous is very similar to *Priodontes*, but the bands are about 30 in all, 6 to 7 forming the scapular shield, 11 to 13 the dorsal shield, and only about 11 the pelvic shield. The dorsal scutes in an individual of *C. unicinctus* are longitudinally or transversely oblong or square; the scapulars are clearly smaller and less regular; the pelvics are like the scapulars, but much larger and larger than the dorsals. The free cervical scutes, cut off from the scapular shield, form about two short bands of irregularly spaced, irregularly shaped, scutes. (Text-fig. 16, p. 993.)

Adults of both these genera have the scutes smooth, polished, hairless, and but little sculptured.

In *Euphractus* and its allies the scutes are also tolerably alike from the neck to the caudal region. They are marked with two grooves converging or confluent in front, and each is pitted with a row of setal pores. Those of the dorsal bands, which are from 6 to 8 in number, are evenly longitudinally oblong and are typically, at all events, larger and more regular in shape than the scapulars or pelvics, which show a tendency to be pentagonal or hexagonal, especially on the lateral slope of the scapular shield

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* This species has been referred to a distinct genus, *Cryptophractus*.

and on the posterior part of the pelvic. The scapular shield exhibits above, excluding the cervicals, from 4 to 5 rows, varying individually, but these are increased to about 8 laterally by the intercalation of additional scutes. Thus in the middle line above there are 4 or 5 scapular bands, 6 to 8 dorsal bands, and about 9 pelvic bands, making about 20 in all, a reduction in the number seen in *Cabassous*. One or two rows in front of the scapular shield, and differentiated from it, constitute cervical bands, varying specifically. In *Euphractus sexcinctus* there is a single very sharply differentiated cervical band composed of 8 or 9 scutes as large as the dorsals or larger, and the first scapular band is fused with the second and level with it. In *Eu. vellerosus* and *nationi* the cervical band is like that of *Eu. sexcinctus*, but the first scapular is separated from the second and raised posteriorly above its level. In *Eu. villosus* and *Zaëdyus pichiy* (*minutus*), the first scapular is similarly separated; but the cervical is reduced to a few small scutes. (Text-fig. 15, p. 991.)

The scutes vary considerably in coarseness of sculpture, being more rugged in a hairy form like *Eu. villosus*—where they are also smaller—than in *Eu. sexcinctus*. In the latter the median scute of three or four of the pelvic bands is differentiated from the rest, and marked with the deep glandular pit I described some years ago (Proc. Zool. Soc. 1913, pp. 1099–1103). In *Eu. villosus* and *vellerosus* these pits may be reduced to two. Probably they are present in all the species referred to *Euphractus*; but in *Zaëdyus pichiy* I can find no trace of them *.

Scleropleura bruneti, described by Milne-Edwards, is an aberrant member of the Euphractine Armadillos characterized by degeneration, or incomplete development, of the scutes and scales, especially over the median area of the head, back, and tail †.

In *Dasypus* (= *Tatusia*) the three regions of the carapace are very sharply differentiated. The scutes of the dorsal shield, 7 to 9 in number, although tolerably similar to those of *Euphractus*, are longer, narrower, and more numerous, with the central space between the grooves forming a polished area shaped like a human incisor tooth. The scutes of the last scapular shield, as in other genera, are like the dorsals; but the rest are very different, consisting of small, closely packed, mostly irregularly arranged plates encircled by a row of pores and smaller scutes. At the anterior end of the scapular shield they are arranged in distinct rows, but there are no differentiated cervical scales. The scutes of the pelvic shield are similar to those of the scapular. The emargination of the posterior border of the pelvic shield over the root of the tail forms in this genus, as in the others already described, an evenly concave excision, about one-third of the circumference of a circle.

* When present these pits are marked by very distinct bony bosses or excrescences on the underside of the pelvic shield. Of these there is no trace in *Zaëdyus*.
† See Anthony, Ann. Sci. Nat. Zool. Paris, (10) v. 1922, pp. 351–363.

In *Tolypeutes* and its allies, the three regions are also sharply differentiated, the scutes are exceedingly thick and, when unworn, coarsely sculptured. The bands of the dorsal shield are from 2 to 4 in number, their component scutes are large, generally speaking oblong and roughened with tubercles separated by radiating grooves. Those of the scapular and pelvic shields are similarly sculptured, but more or less hexagonal in shape. The cervical scutes are at most represented by a few small tubercles. The scapular shield consists of 8 bands above, increasing to about 12 laterally, and the pelvic of about 17 or 18. Thus there are about 30 bands in all along the middle line of the back. The caudal emargination of the very large strongly convex pelvic shield is much deeper and more rectangular than in the other genera.

A peculiarity of the carapace of *Tolypeutes*, as compared with that of the genera already described, is its partial freedom from the body, so that in the scapular and pelvic regions there is a large lateral chamber into which the fore and hind limbs respectively are tucked away when this Armadillo practises its defensive habit of rolling into a compact ball, with the head and the tail, lying side by side, blocking the space formed by the concavity of the median portions of the edges of the scapular and pelvic shields. The lateral scapular and pelvic spaces are separated by an integumental band passing from the sides of the body to the free dorsal scutes of the carapace. The scapular space is open in front; but the pelvic space is bounded behind by a similar but smaller band, which extends outwards to the posterior angle of the pelvic shield from the circumanal area. This band is the anterior border of a small caudal space in which the base of the tail is imbedded *. (Text-fig. 35, D, p. 1024.)

The partial freedom of the carapace seen in *Tolypeutes* is carried to an extreme in *Chlamyphorus*, in which the undifferentiated dorsal and scapular shields are only attached to the body by a thin longitudinal strip of membrane along the middle line of the back. Hence these portions of the carapace hang as a continuous free flap, which is flexible owing to the thinness of the plates, over the densely hairy sides of the body, with a narrow space between. In front, however, this space comes to an end a little behind the ear, the cervical bands being thicker and fused throughout their width to the nape of the neck. The thinness and flexibility of the scutes does away with the necessity for a special joint between the dorsal and scapular regions.

The pelvic shield, however, is sharply marked off from the dorsal. It forms a nearly vertical, nearly simicircular disk, giving the characteristic truncated appearance to the posterior

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* For a full account of the external and internal anatomy of this genus see Murie, Trans. Linn. Soc. xxx. p. 71; also Garrod, Proc. Zool. Soc. 1878, pp. 222–230.

end of the body. It is composed of 6 concentric rows of firm hard scutes, with fringes of soft silky hairs projecting between those of the upper rows. The inferior row forms a half-circle round the narrow caudal notch. Although this pelvic shield is attached above to the bones of the pelvis, it is separated from the body inferiorly by a space divided below superficially by the circumanal area, which passes from the perinæum to the root of the tail. (Text-fig. 34, C, p. 1023.)

In the peculiar differentiation of the pelvic shield, in the unbroken continuity between the cephalic, scapular, and dorsal bands, and the looseness and flexibility of the greater part of the carapace, *Chlamyphorus* differs from all other Armadillos. But the related genus *Burmeisteria* shows an analogy to *Scleropleura* in the degeneration of its exoskeleton, the centre of the pelvic shield being composed of soft skin and its marginal scutes separated from each other (see Anthony. *tom. cit.*).

By the characters of the carapace the principal genera of the Armadillos may be distinguished as follows:—

a. Scapular and dorsal scutes forming an undifferentiated series of movable transverse bands, the scapulars confluent in front with the cephalic shield; the pelvic shield forming a vertical, nearly flat, semicircular disk, with narrow caudal notch; the dorsal and scapular bands overhanging the sides of the body, to which they are attached along the spine by a narrow strip of integument; sides and ventral surface of body thickly covered with soft hair, without scutes . . . . *Chlamyphorus.*

a'. Scapular scutes forming a rigid shield separated from the head-shield in front and the pelvic shield behind by a varying number of free dorsal bands; pelvic shield strongly convex from side to side and back to front, not a semicircular disk, the caudal notch wide; sides and ventral surface of body scantily hairy.

  b. Dorsal area short, with only from 2 to 4 bands; pelvic shield very large, strongly convex and, like the scapular shield, free to a great extent from the underlying regions of the body, thus forming a deep recess into which the fore and hind limbs are tucked away; body capable of being rolled into a compact sphere . . . . *Tolypeutes.*

  b'. Dorsal area longer, with at least 6 free bands; scapular and pelvic shields adherent to the body almost to the base of the limbs; body incapable of rolling into a compact sphere.

    c. Scutes of scapular and pelvic shields relatively small and quite unlike those of the dorsal shields; cervical scutes undeveloped . . . . *Dasypus.*

    c'. Scutes of scapular and pelvic shields larger and tolerably similar to those of the dorsal bands; one or more rows of cervical scutes between the scapular and head-shields.

      d. From 6 to 8 dorsal bands and 1 cervical band; sculpturing of scutes coarser . . . . *Euphractus, Zaëdyus.*

      d'. From 11 to 13 dorsal bands and 3 to 4 cervical bands; scutes less coarsely sculptured, often smooth and polished . . . . *Cabassous, Priodontes.*

c. *The Tail-scutes of the Armadillos.*

The caudal scutes attain their highest grade of development in *Dasypus* (*Tatusia*), where in the basal portion of the tail they

form definite rings, each composed of a mosaic of three trans-
verse rows of closely-fitting plates. This portion of the tail is
definitely jointed, the rings being separated by flexible arthrodial
membrane. The distal portion of the tail is not segmented, the
scutes being irregularly arranged, the transition between the
segmented and unsegmented portions being gradual. (Text-
fig. 14, D.)

In *Euphractus* and its allies the tail is somewhat similarly

Text-figure 14.
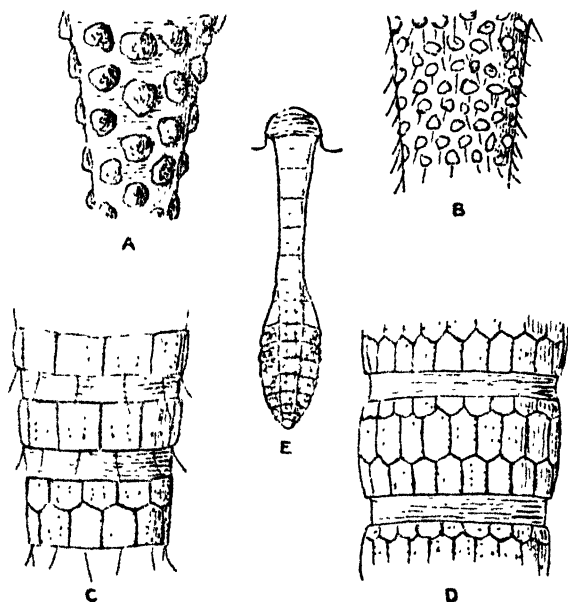
A. Portion of proximal half of tail of *Tolypeutes mataca*.

B. The same of *Cabassous unicinctus*.

C. The same of *Euphractus sexcinctus*.

D. The same of *Dasypus novemcinctus*.

E. Entire tail of *Chlamyphorus truncatus*.

segmented proximally and unsegmented distally, but the rings of
the segmented portion consist of from one to two rows of scutes.
(Text-fig. 14, C.)

In *Priodontes* no part of the exoskeleton of the tail is definitely
segmented, the scutes being tolerably uniform in size, close-set,
and arranged in irregular transverse rows. In *Cabassous* also
the tail is unsegmented, the scutes, even when most apparent,
being small, separated, and irregularly arranged. In some

cases they are almost entirely suppressed, a condition which suggested for this genus the now obsolete name *Lysiurus*. (Text-fig. 14, B.)

In *Tolypeutes* the tail is unsegmented, the scutes of the upper side forming irregular rows of large elevated tubercles, whereas on the lower side they are flat. (Text-fig. 14, A, and 35, D.)

In *Chlamyphorus* the scutes of the tail are defective for the most part, although retained as small scales on the terminal spatula. (Text-fig. 14, E.)

Other features of the tail in Armadillos and the distinguishing characters of the genera of this group as indicated by this organ are described below (p. 1020).

d. *The Head-shield of the Armadillos.*

The head-shield extends from the upper surface of the snout, where the scutes are smaller and less differentiated, backwards to the region of the ears, passing above the eyes on each side. I have no data enabling me to judge which is the most primitive type.

In *Cabassous* it is tolerably evenly oval in outline, and consists of a comparatively small number of tolerably large smooth plates, sometimes irregularly, sometimes subsymmetrically, arranged, the marginals being smaller than the medians.   But even within specific limits there is often marked variation in the size, number, and subdivision of the scutes.   The marginal scutes towards the base of the ears appear to be continuous with the integument, and do not project as a free edge.   In *Priodontes*, on the other hand, judging from the mounted specimens I have seen, the scutes at the sides of the shield between the eye and the base of the ear project to a small extent.   In other respects this genus does not appear to differ in any important respect in the structure of the head-shield from *Cabassous*.   (Text-fig. 16, A.)

In *Euphractus* and its allies the head-shield is expanded behind and projects somewhat in front of the base of the ears, where it is usually concave.   The scutes vary in number, size, and sculpture individually and specifically.   In *Eu. sexcinctus*, for instance, they are larger, fewer, and smoother than in *Eu. villosus*, *Zaëdyus pichyi*, resembling the latter in these respects. (Text-fig. 15, A.)

In *Dasypus* (= *Tatusia*) the head-shield is elongated and somewhat piriform, and its posterior edge is angularly pointed in the middle.   It consists of a large number of small irregularly-shaped scutes.   (Text-fig. 15, C.)

So far as the size, symmetry, and regularity of arrangement of the scutes are concerned, *Tolypeutes* possesses the highest type of head-shield.   On its anterior portion in front of the eyes the scutes are smaller and irregularly placed; but its posterior portion consists of large marginal and central scutes, the latter

forming at most a double row. The postero-lateral and posterior margin is tolerably evenly convex and projects backwards some distance beyond the base of the ears as a free occipital ridge. (Text-fig. 15, B, and 17, F.)

The head-shield of *Chlamyphorus* differs from that of all the

Text-figure 15.
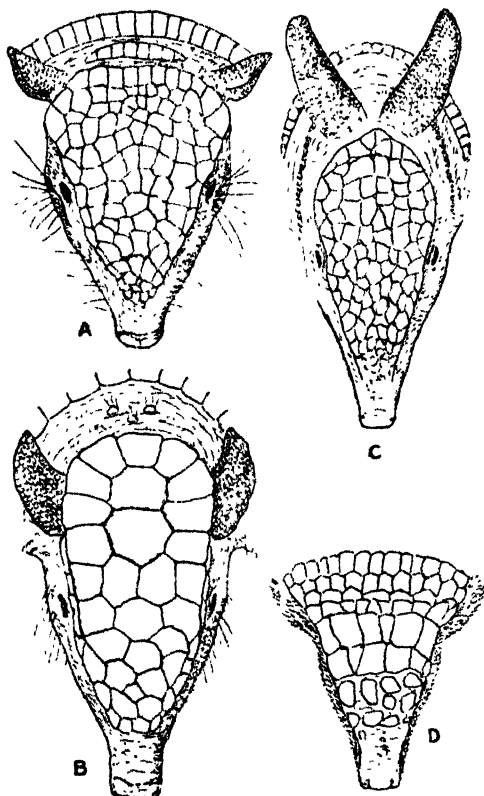
A. Upper view of the head and neck of *Zaedyus pichyi* (*minutus*), showing the characteristics of the *Euphractus*-group.

B. The same of *Tolypeutes mataca* (*conurus*).

C. The same of *Dasypus novemcinctus*.

D. The same of *Chlamyphorus truncatus*.

foregoing in being confluent with the scapular shield. It consists of transverse rows of scutes varying in size, shape, and arrangement within specific limits, and its lateral margin in front is partially free from the head for a space reaching nearly as far back as the eye. (Text-figs. 14 D, 18 A.)

The principal characters of the head-shield differentiating the chief genera of Armadillos may be epitomised as follows :—

a. Head-shield continuous behind with cervical and scapular shields, free from the head for a short distance in front of the eye .... *Chlamyphorus.*
a'. Head-shield not confluent with cervical or scapular scutes.
  b. Scutes large and mostly symmetrically arranged in 3 or 4 median and lateral rows .... *Tolypeutes.*
  b'. Scutes large or small, not symmetrically arranged in 3 or 4 median and lateral rows.
    c. Posterior border of shield angularly pointed behind ; scutes many and comparatively small .... *Dasypus.*
    c'. Posterior border of shield convex or nearly straight.
      d. Head-shield evenly oval, not expanded between the eyes and ears ... . *Cabassous, Priodontes.*
      d'. Head-shield not evenly oval, expanded on each side between the eye and ear ... . *Euphractus, Zaëdyus.*

THE HEAD AND ITS ORGANS.

a. *The Head of the Armadillos.*

In Armadillos the head itself, as is well known, is conical, broad at the occipital region, and tapering to the snout, which is relatively longer and narrower in *Dasypus* than in other forms. The gape of the mouth is long.

The *facial vibrissæ* are always reduced in length and number on the snout and generally elsewhere. In all the genera, except *Euphractus* and its allies, they seem to be absent or practically functionless if vestiges remain. But in *Euphractus* and *Zaëdyus* there is a well-developed genal tuft consisting of long vibrissæ just beneath the eyes and directed forwards and upwards as if to guard those organs. There is also a small genal tuft in *Toly-peutes.* The interramal tuft is also present and moderately well developed in *Euphractus* and *Zaedyus*, and a few short mystacials are retained far back on the upper lip between the eye and the rhinarium, and sometimes, at all events, there are one or two small superciliary vibrissæ. (Text-fig. 17, A, F.)

In the retention of some of these vibrissæ, *Euphractus* and *Zaëdyus* are more primitive than the other genera and resemble *Orycteropus.* The rest resemble the *Pholidota* in the suppression of these bristles.

The *rhinarium* is naked and moist, and varies but little in different genera. It is not sharply defined above or laterally, and has a lightly convex upper edge with rounded angles. The nostrils are anterior with reduced lateral slit, and are separated by an ungrooved, moderately broad septum. To the admedian edges of the septum in *Euphractus* are attached two soft movable flaps of integument which abut against somewhat similar flaps jutting into the nostrils from their outer edges, the two acting conjointly as valves to close the orifices. In *Tolypeutes, Dasypus* (*Tatusia*), and *Chlamyphorus* there is a single valvular flap running downwards and inwards into the nostrils from their upper edges. (Text-figs. 16, D ; 17, C, D, G ; 18, B.)

This method of closing the nostrils by valvular flaps set within the orifices is quite different from the method described in *Orycteropus* (P. Z. S. 1924, p. 699).

In connection with the mouth it may be noted that in

Text-figure 16.
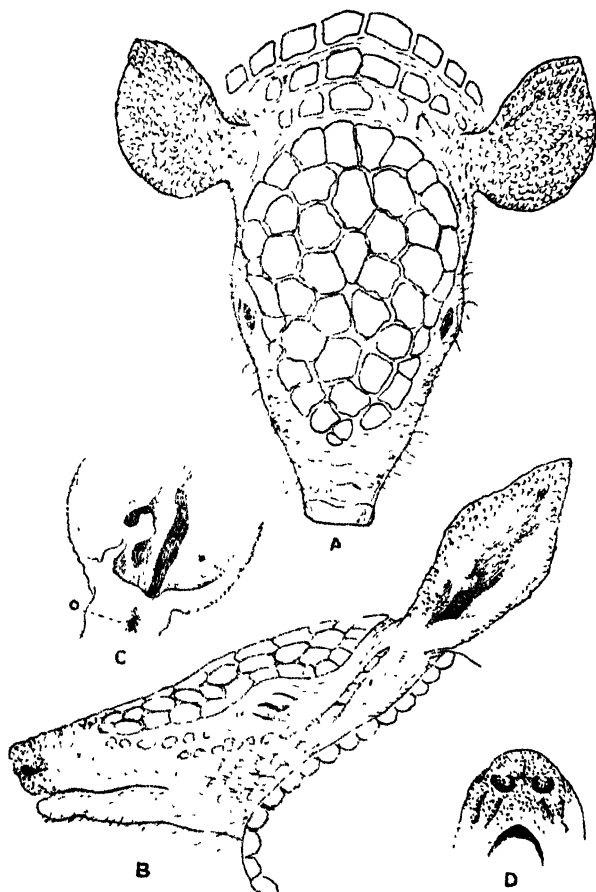
A. Upper view of head and neck of *Cabassous unicinctus*.
B. Side view of head of *Dasypus noremcinctus*.
C. Base of ear of the same, showing the ridges and grooves and the orifice (*o*) set low down in the concealed tubular portion.
D. Rhinarium of the same.

Chlamyphorus the upper lip shows below the rhinarium a small pendulous lobe on each side, which seems to be unrepresented in other genera. (Text-fig. 18, A.)

The *ears* are typically normally situated wide apart on each side of the head behind the ear; but in *Dasypus* (*Tatusia*), as is well known, they rise close together on the occipital region

Text-figure 17.
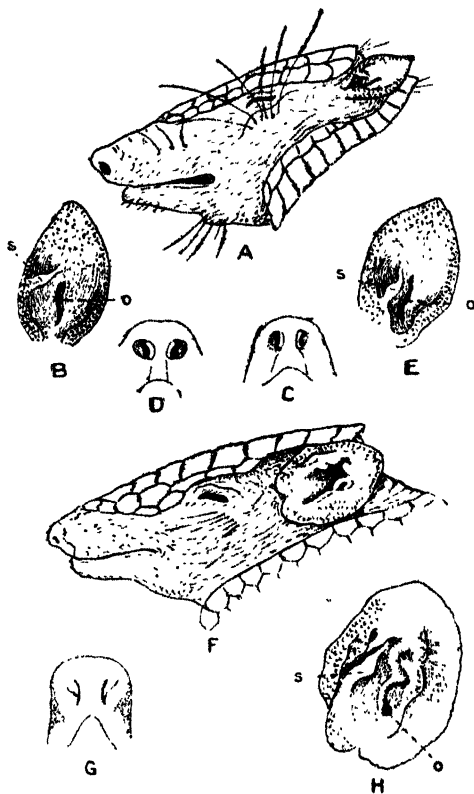
A. Side view of head of *Zaëdyus pichyi*, showing the genal and interramal tufts of vibrissæ.

B. Ear of the same, showing the supratragus (*s*) and the valvular slit (*o*) containing the orifice.

C. Rhinarium of the same.

D. Rhinarium of *Euphractus sexcinctus*.

E. Ear of *Euphractus villosus* (lettering as in B).

F. Side view of head of *Tolypeutes mataca*, showing a small tuft of genal vibrissæ, the absence of interramal vibrissæ, and the basally expanded ear.

G. Rhinarium of the same.

H. Ear of the same (lettering as in B and E).

behind the margin of the head-shield. In *Euphractus* and its allies they vary in size, being moderately large in *Eu. sexcinctus*, and much smaller in *Eu. villosus* and in *Zaëdyus*. They are

narrow and, to a small extent, tubular and mobile at the base, with evenly convex posterior margin and angular tip, the anterior margin being convex, at all events towards the base. They are comparatively simple in structure, the vertically slit-like orifice in the lower half of the cavity, above the inferior junction of the thickened anterior and posterior rims of the pinna, being defined in front and behind by small soft flaps of skin which meet over the orifice when it is closed. The only other structure concerned in the closing of the ear is a short ridge jutting backwards from the anterior edge and ceasing close to the upper end of the auditory slit. Perhaps this represents the supratragus of other mammals. There is no definite tragal or antitragal thickening defining the inferior notch. (Text-fig. 15, A; 17, A, B, E.)

Text-figure 18.
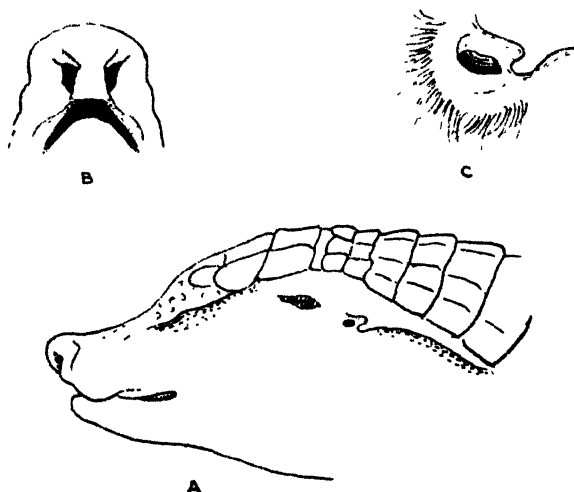
A. Side view of head of *Chlamyphorus truncatus*, the hair omitted to show the minute ear close to the eye.
B. Enlarged view of the ear of the same.
C. Front view of rhinarium of the same.

In *Tolypeutes* the ear is more sessile than in *Euphractus*, and is attached by a broader base to the side of the head, but the attachment is concealed by a laminate downward extension of the lower portion of the pinna. It is also more evenly oval, and its cavity is more complicated by ridges and grooves. The flap-like margins of the auditory slit are larger, and in front of the anterior flap there is a vertical depression into which the anterior ridge projects upwards and backwards as a small fleshy lobe; but this does not rise from the anterior edge of the pinna, but well

within its margin. Above the upper end of this there are two somewhat similar soft, thick ridges directed downwards and defined by deep grooves. (Text-fig. 15, B; 17, F, H.)

In *Dasypus* the ear, set high up on the back of the head, is much longer, more expanded, and basally more tubular than in *Euphractus*. It is also more complex in structure. The anterior ridge, as in *Tolypeutes*, is a fleshy lobe far removed from the anterior margin of the pinna. Posteriorly it juts into the cavity, ceasing in front of the auditory slit, and abutting, when the ear is closed, against the well-developed posterior flap bordering the slit behind. Above the lobe there is, at all events sometimes, another ridge forcibly suggesting the supratragus of most other mammals, and below it in front of the notch may be seen a small process like the tragus, while the antitragus seems to be represented by a small prominence continuous above with the posterior flap of the auditory slit. This appears to me to be the least degenerate type of ear seen in the Armadillos. (Text-fig. 15, C; 16, B, C.)

By far the most degenerate type is seen in *Chlamyphorus*, where the ear, situated close behind the eye, is represented by an oval orifice surmounted by a small ridge of integument ending behind in a pendulous lobe, behind which a short flap extends backwards to the carapace attaching the scutes above it to the integument. In the structure of the ear *Chlamyphorus* stands quite alone in this group of Edentates. (Text-fig. 18, A, C.)

b. *The Head of the Anteaters.*

The head of the Anteaters is peculiar on account of the down curvature of the muzzle, so that the nose is below the level of the eyes. The variation is marked even in *Cyclopes*, in which the muzzle is comparatively short and normal. It is noticeable also in the young of *Tamandua* and *Myrmecophaga*, although less pronounced than in the adults. (Text-figs. 19, A ; 20, A, D.)

The *facial vibrissæ* are represented at most by a few short delicate bristles on the lips and nose, the superciliary, genal and interramal tufts being absent, as in the Pholidota and some Armadillos.

The *rhinarium* is naked and moist, but is not sharply differentiated from the skin of the muzzle either laterally or above. Its upper edge is convex, and it is as broad below the nostrils as above. The nostrils are normal, consisting of a postero-lateral slit and an antero-internal expanded portion opening forwards. The internarial septum is moderately wide and marked in *Tamandua* and *Cyclopes* with a median sulcus, which is much less distinct in *Myrmecophaga*. The infranarial portion has some additional grooves in *Cyclopes*. (Text-figs. 19, C, D; 20, B, E.)

In these animals the rhinarium is more normal than in the Armadillos, and the nostrils have not acquired the valvular flaps described in the latter.

The *mouth* has a relatively short gape, its angle only extending a short distance behind the rhinarium. It is relatively longer in *Cyclopes* than in *Tamandua* and *Myrmecophaga*. Both in

Text-figure 19.
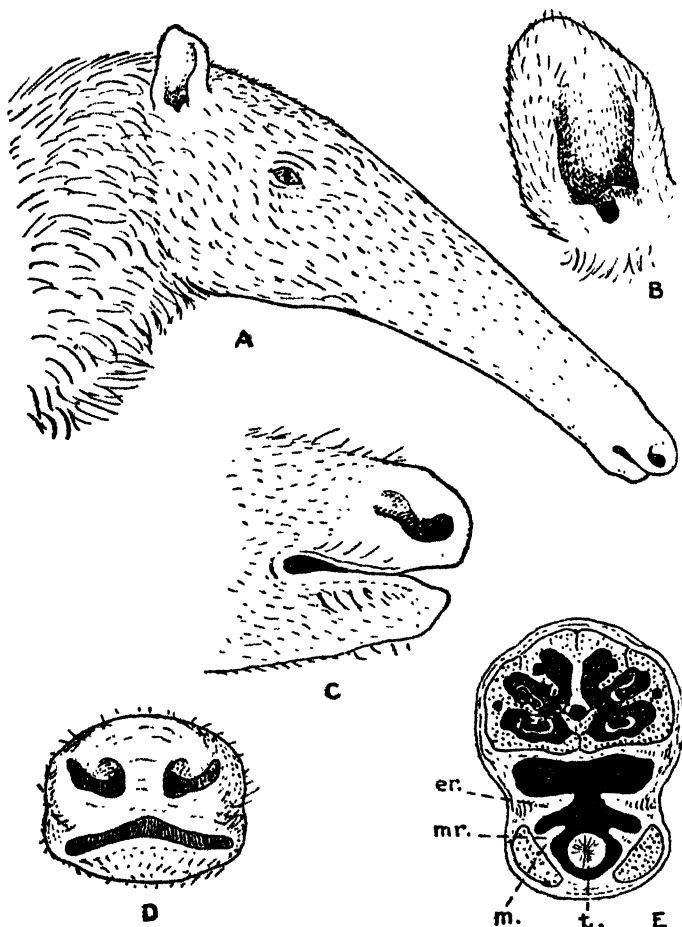
A. Head of young *Myrmecophaga tridactyla*.
B. Ear of the same.
C. Side view of the end of the muzzle of the same.
D. Front view of the muzzle of the same.
E. Transverse section of the muzzle, showing the groove for the tongue (*t*) ;
    m, mandible ; *mr*, ridge on gum of mandible; *er*, ridge on cheek.

Tamandua and *Myrmecophaga*, but not, I think, in *Cyclopes*, the tongue runs along a deep channel between the two halves of

Text-figure 20.
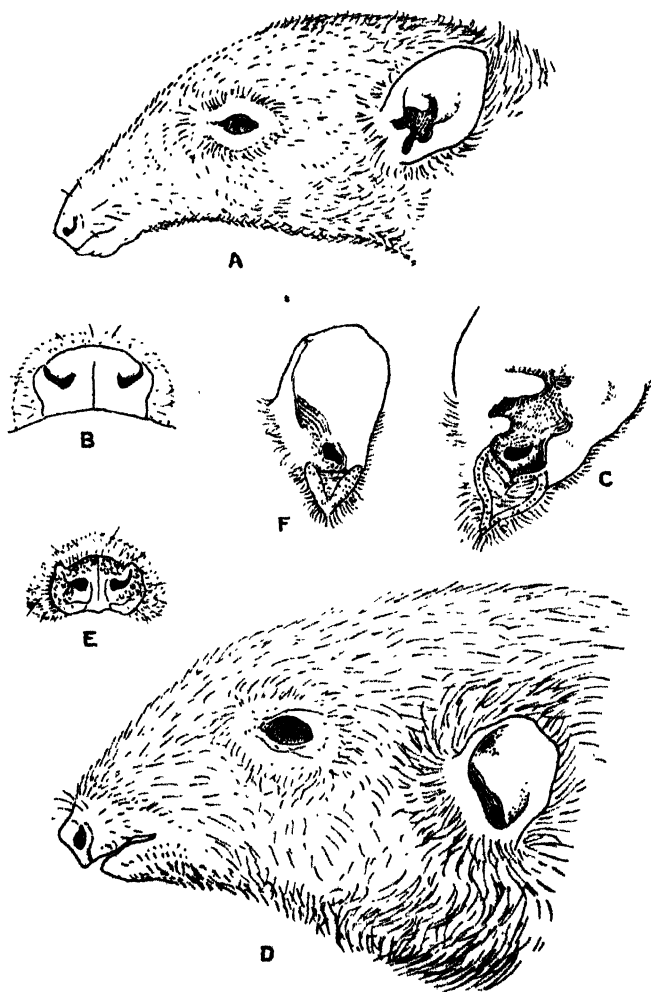
A. Side view of head of young *Tamandua tetradactyla*.

B. Front view of rhinarium of the same.

C. Base of ear of the same, vertically cut in the intertragal notch to show
   the orifice.

D. Side view of head of adult *Cyclopes didactylus*, with the hairs parted
   to reveal the ear.

E. Rhinarium of the same from the front.

F. Ear of same, vertically cut below the orifice.

the mandibular rami, and this channel is partially overlapped above by a long shelf-like flap arising from the mandibular gum, and extending backwards within the mouth nearly as far as the level of the eye. This lingual channel is in addition roofed over and separated from the palate by two large ridges, developed on the epithelium of the cheek, one on each side. These project freely into the cavity of the mouth and meet in the middle line, dividing the mouth into an upper and a lower portion, the latter containing the tongue. These ridges are attenuated in front and behind, are shorter than the ridge on the mandibular gum, and are closely beset with backwardly directed spicules which presumably help in the swallowing of ants. (Text-fig. 19, E.)

The *ears* are not large. In *Tamandua* and *Myrmecophaga* they stand well away from the head, to which they are attached by a tolerably wide base. In *Tamandua* they are tolerably evenly oval with a deepish cavity and the anterior edge not over-folded. The intertragal notch (*inferior meatus*) is well defined by a tragal lobe in front and an antitragal lobe behind. Above the tragus there is an angular process, and above this again a rounded lobe, which forms the greater part of the upper margin of the cavity. The latter is defined behind by a ridge, on the outer side of which is another ridge showing a rounded lobe above the antitragus. (Text-fig. 20, A, C.)

The ear of *Myrmecophaga*, although set higher on the head, is tolerably similar in shape to that of *Tamandua*, but in the specimen examined by me was somewhat simpler in structure. The cavity was less well-defined above, in front and behind, and the lobes and notches were not so clearly marked. But Boas's figure of the ear in this genus agrees very closely with the ear of *Tamandua* described above. (Text-fig. 19, B.)

In *Cyclopes* the naked ear is set noticeably below the level of the eye, is reduced in height, and is completely concealed by the adjoining long hairs of the head. It is attached to the head by a very wide base. The anterior rim is slightly overfolded. The cavity is represented by an obliquely elongated slit at the bottom of which lies the large auditory aperture. This slit is bordered in front by a ridge continuous with the overfolded anterior rim of the pinna, but there are no definite tragal, or antitragal, or other lobes, and the inferior meatus is wide. In this genus the upper part of the pinna folds down over the lower half. (Text-fig. 20, D, F.)
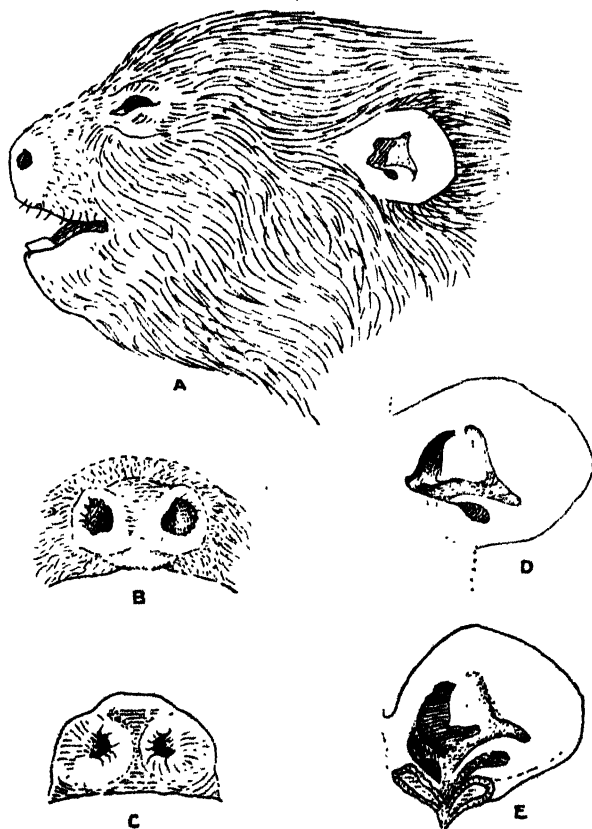
c. *The Head of the Sloths.*

In the Sloths the head is covered on the crown and cheeks with long hair. The muzzle is short, deep, and truncated, and clothed with short hair. The lower jaw is particularly massive as compared with that of the Anteaters and Armadillos, and the gape of the mouth is long, extending backwards on each side as far as the level of the eyes, which are bulging and look nearly directly forwards. (Text-figs. 21, A; 22, A, B.)

The *facial vibrissæ* are practically aborted, a few short soft hairs on the upper lip alone persisting to represent the mystacials.

The *rhinarium* is markedly different in the two genera. In *Bradypus* it is a comparatively small, naked, smooth area, at most

Text-figure 21.

A. Side view of the head of *Cholœpus*, with the hair parted to reveal the ear.
B. Front view of rhinarium, with nostrils expanded (from a dried skin).
C. The same, with nostrils partially closed.
D. Ear of the same, the dotted lines showing the points of attachment of the pinna.
E. The same, with the inferior portion cut to reveal the orifice.

defined by a shallow groove from the skin of the upper lip and nose. When this groove is distinguishable (in a young specimen) the shape of the rhinarium can be seen. Its upper edge is convex, and the infranarial portion is constricted in the middle,

so that its narrowest portion is only equal in width to the internarial septum. The nostrils are subcircular orifices opening forwards, and differing from those of the Anteaters in having no postero-lateral notch.

In *Cholœpus* the rhinarium is relatively large and well developed. The nostrils are tolerably widely separated and have

Text-figure 22.
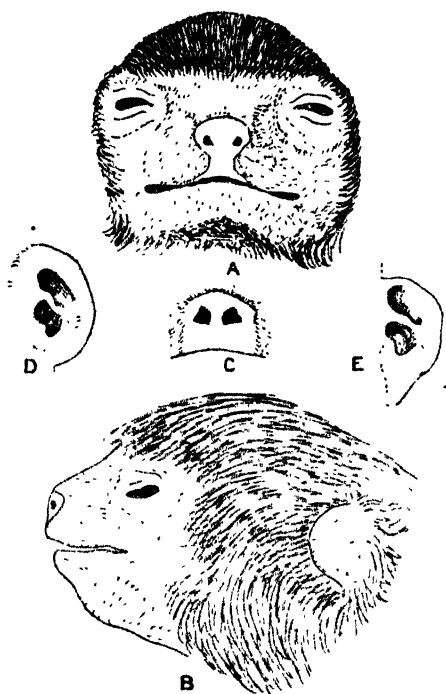
A. Front view of head of a young *Bradypus tridactylus*.
B. Side view of the same, with hairs parted to show the normal position of the ear folded forwards.
C. Front view of rhinarium of an adult specimen.
D. Ear of the same turned backwards, the dotted lines showing points of attachment of pinna.
E. The same, with its basal portion slit to show the shallow inferior cavity.

thickened constricting rims, so as to be capable of expansion and contraction. The rims are sculptured with radiating grooves and ridges, and the internarial area, which is depressed owing to the thickening of the inner edge of the nostrils, is transversely grooved and ridged. (Text-fig. 21, A, B, C.)

The *ears* of *Bradypus* and *Cholœpus* differ considerably. They are hairy and completely concealed beneath the skin of the sides

of the head * as in *Cyclopes*, the essentially arboreal anteater. They are set a considerable distance behind the eye and low down, as in *Cyclopes*; and in *Bradypus* at least appear to be normally closed by the folding of the flap of the pinna over the orifice.

In *Cholœpus* † the ear is comparatively large, thick, and complex, attached by a wide base and standing well away from the head. It has a tolerably evenly convex or somewhat angular edge, and is longer than high. The posterior part of the pinna forms a nearly flat lamina, with a simple margin; but the anterior part containing the orifice is deeply excavated, the anterior and inferior borders of the cavity meeting at a right angle, forming the intertragal notch or *aditus inferior.* The cavity is partially blocked by two ridges. The upper, probably the supratragus, rises from the upper end of the anterior rim of the cavity and descends downwards and backwards as a triangular or somewhat rounded lobe. Above and behind it the cavity is shallow, below and in front of it it is deep. The second ridge, sometimes continuous posteriorly with the posterior end of the other, is inferior and narrower and longer, and runs forwards and downwards from the posterior lamina of the pinna, narrowing as it goes, and ceases deep in the cavity behind the concealed auditory aperture, which is itself surmounted by a thickened ridge. Behind the aperture and beneath the anterior end of the inferior ridge there is a small but deep and conspicuous pit. There is no definite trace of tragus or antitragus. (Text-fig. 21, D, E.)

In *Bradypus* the ear is relatively smaller and higher as compared with its length than in *Cholœpus*. It is also thicker, more fleshy, and more closely adherent to the side of the head. Its free edge is evenly convex, and there is no posterior laminate expansion of the pinna. Almost the whole of it is occupied by a cavity, which is completely divided into an upper and a lower portion by a ridge of softer integument, the *supratragus*. The lower cavity, containing the orifice, is shallow and simple as compared with the corresponding portion of the cavity in *Cholœpus*. (Text-fig. 22, D, E.)

By the characters of the head enumerated in the foregoing section, the South American· Edentates may be classified ·as follows :—

a. Head short, deep and rounded; muzzle heavy, abbreviated, and truncated, with massive lower jaw; eyes and nostrils directed more forwards on the face .... SLOTHS.
b. Hair of crown directed backwards, not sharply distinguished from that of the face; nostrils larger, with thickened margins; ears with cavity above the orifice closed by a large valve, beneath which there is a ridge curving downwards and forwards ....,............................. .... *Cholœpus.*

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* Flower's statement that they are "inconspicuous" is wholly misleading, if, in a sense, true.

† I cannot quite reconcile my observations on the ear in this genus with Boas's figure (Die Ohrknorpel, etc., pl. xx. fig. 216).

b'. Hair of crown directed forwards and sharply distinguished
    from that of face; nostrils smaller, without thickened
    rims; ear simple, the cavity divided by a single supratragal
    ridge   ... ...   *Bradypus, Scæopus.*

c'. Head elongated, with narrowed elongated snout and slender
    lower jaw; eyes looking sideways, not forwards.

   c. Snout curved downwards, gape of mouth very short, rhina-
       rium normal, nostrils without accessory lobes . .   ANTEATERS.

    d. Head covered with long silky hair entirely concealing the
       short ears, which have a broad base and no accessory
       ridges; snout short, the eyes nearly equidistant from
       the nose and ear   ..   .. *Cyclopes.*

    d'. Head covered with short normal hair; ears prominent,
       longer than wide, with narrower base and defined ridges;
       snout long, the eye in the adult much nearer the ear
       than the nose.

      e. Snout moderately long   ... ... *Tamandua.*
      e'. Snout very long   ..   ... *Myrmecophaga.*

c'. Snout projecting almost straight forwards, the eyes nearly
    in line with the nose, the nostrils of which are provided
    with at least one accessory valvular flap ...   ARMADILLOS.

   f. Ear close to eye; the pinna reduced to a minute ridge and
     lobe above the orifice; face covered thickly with soft
     hair   .   .   .   .   . *Chlamyphorus.*

   f'. Ear some distance behind eye, with well-developed pinna;
     face scantily hairy.

    g. Ears very long, pointed, set close together on the back
      of the head, the orifice concealed in the basal tubular
      portion; snout long and slender   .   . *Dasypus.*

    g'. Ears shorter, set wide apart on the sides of the back of
      the head, the orifice not concealed in the basal tubular
      portion; snout shorter and thicker.

      h. Ears with a broad base, which is concealed by a down-
       wardly directed extension of the area beneath the
       orifice; its cavity with a complex of ridges and
       grooves   ...   . *Tolypeutes.*

      h'. Ears narrowed at the base, which is not concealed,
       the cavity with a simple supratragal ridge and a
       deep valvular groove containing the orifice *.

       j. Interramal and genal tufts of vibrissæ well de-
        veloped   ...   . *Euphractus, etc.*

       j'. Interramal and genal tufts of vibrissæ incon-
        spicuous or absent   ... . *Cabassous, Priodontes.*

THE FEET.

a. *The Feet of the Armadillos.*

The *fore foot* is typically five-toed and asymmetrical. In
Euphractus, Zaëdyus, and their allies the digits are united
approximately up to the base of the digital pads, although the
latter are seldom well defined. They are therefore capable of
a certain amount of lateral separation. Excluding the claws,
the 2nd digit is the longest. It is armed with a long strong
claw; but the 3rd, which is a little shorter, measured to
the pad and usually thinner, carries a longer claw, the tip of
which reaches the level of that of the 2nd. The 4th is much
shorter than the 3rd, and the 5th than the 4th, the 5th being
situated about halfway between the carpus and distal end of the

* This statement regarding the ears is only doubtfully true of *Cabassous* and
Priodontes, of which I have only seen dried skins.

sole. It carries a moderate claw, much smaller than that of the 4th, which approximately equals the claw of the 3rd in size. These four digits are tolerably evenly spaced and, generally speaking, show a progressive decrease in size from the 2nd to the 5th. The 1st is about equal to the 5th in length, but has a weaker claw and arises some distance behind the 2nd, nearly on a level with the 4th or a little behind that point.

The sole is covered with naked wrinkled skin, and has no pads. Scattered hairs project in the interdigital spaces from the 2nd to the 5th, and on the outer side of the sole behind the 5th; but the inner side of the foot has a fringe of long hairs. Behind the sole there is a prominence carrying a tuft of hairs representing the carpal vibrissæ of normal mammals. (Text-fig. 23, A, B.)

The fore foot of *Cabassous* (= *Xenurus*, *Lysiurus*) is an exaggeration of that of *Dasypus* and its allies. It is more specialised for digging. The digits, apart from the 2nd, are more completely fused and less mobile. The 1st is set far forwards on the inner side of the sole on a level with the 3rd, and the pad of the 2nd projects a long way beyond that of the 3rd. The 3rd and the 4th carry great blade-like claws, far exceeding in length, thickness, and depth the relatively slender claw of the 2nd. Thus, in *Cabassous* the fossorial work is performed mainly by the great claws of the 4th and 5th digits, the 2nd playing quite a subsidiary part, whereas in *Euphractus*, the work is thrown tolerably equally upon the claws of the 2nd, 3rd, and 4th digits. *Euphractus* has a more generalised foot better fitted for running than that of *Cabassous*, the claws being relatively smaller and the digits less fused. (Text-fig. 23, C, D, E.)

Judging from a mounted specimen the fore foot of *Priodontes* is tolerably similar to that of *Cabassous* in the fusion and relative position and size of the digit; but in this case the claw of the 3rd digit, which is prodigiously long, stout, and curved, and greatly exceeds that of the 4th, is the dominant digging tool. It is a more specialized type of foot than that of *Cabassous*; and the sole is said to be scaly; but I have not been able to examine the underside of the foot.

The fore foot of *Chlamyphorus* conforms tolerably closely to that of *Cabassous* in the relative lengths, position, and degree of fusion of the digits; but there is less inequality in the claws, those of the 1st, 2nd, and 5th digits being relatively longer and stronger. The large size of the 5th is particularly noticeable, and this is associated with the development of a pad-like carpal prominence on its under and outer side. The carpal vibrissæ seem to be absent in this aberrant genus. (Text-fig. 24, A.)

The fore foot of *Tolypeutes* may also be derived from that of *Euphractus*, but the variations have taken a different direction from those of the genera noticed. The 1st digit is greatly reduced, sometimes absent, and, when present, is situated high up the foot near the carpus. Its claw is often minute and probably

functionless. The 2nd, measured to its terminal pad, is much longer than the 3rd and capable of greater freedom of movement than in any Armadillo. Its claw is only moderately long and strong. The 3rd is fused up to the terminal pad but carries a great falcate claw, the tip of which reaches the level of that of the 2nd. The 4th digit is a little larger than the 1st, and

Text-figure 23.
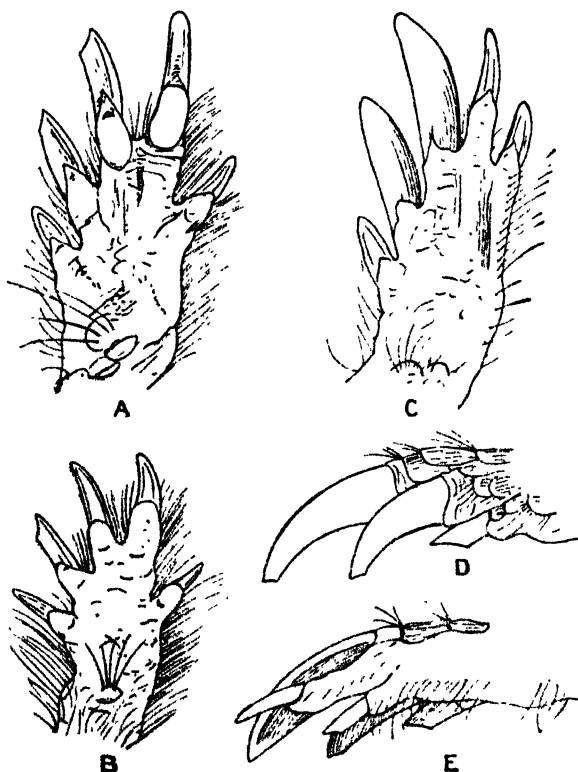
A. Right fore foot of *Euphractus sexcinctus* from below.
B. The same of *Zaëdyus pichyi*.
C. The same of *Cabassous unicinctus* (from a dried skin).
D. The same from the outer side, showing the 3rd, 4th, and 5th digits.
E. The same from the inner side, showing particularly the 1st and 2nd digits.

carries a larger or smaller claw. The 5th, when present, is quite small.

In this Armadillo digging is performed practically entirely by the claws of the 2nd and 3rd digits. The genus differs entirely from other genera in mode of progression, since it rests upon

66*

the tips of the claws of the 2nd and 3rd, the entire sole and the 1st and 4th digits being raised from the ground.

Within the limits of this genus, as at present understood, the number of digits varies. In *T. tricinctus* there are five, as in typical Armadillos. In *T. mataca* (=*conurus*) there are four, the 5th being lost. In *T. muriei* there are but three, the 1st and 5th

Text-figure 24.
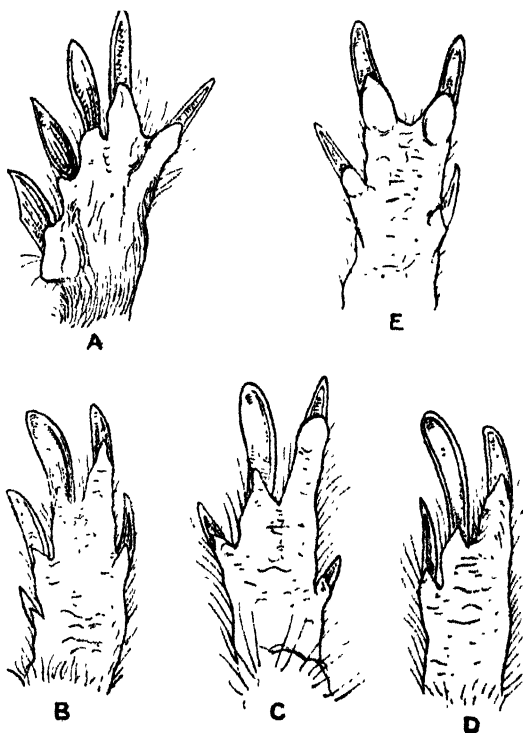
A. Right fore foot of *Chlamyphorus truncatus*.
B. The same of *Tolypeutes tricinctus*.
C. The same of *T. mataca*, showing the suppression of the 5th digit.
D. The same of *T. muriei*, showing the suppression of the 5th and 1st digits.
E. The same of *Dasypus novemcinctus*, showing the 3rd digit slightly surpassing the 2nd, the 5th being suppressed.

being suppressed. This suppression of digits is associated with the peculiar method of walking mentioned above, the position in which the foot is held raising the 1st and 5th digits high off the ground and rendering them functionless for support. (Text-fig. 24, B, C, D.)

The fore foot of *Dasypus* (*Tatusia*) can also be derived from

that of *Euphractus*, but here again the variations have taken a different direction. The foot is subsymmetrically four-toed, the 5th digit being absent externally, and the 1st and 4th and the 2nd and 3rd respectively subequal and approximately on a level. The 1st and 4th digits are placed, as regards the 2nd and 3rd respectively, practically as in *Euphractus*; but the 3rd, instead of being shorter and weaker than the 2nd, is as long as it or slightly longer, and carries a subequal claw. (Text-fig. 24, E.)

Text-figure 25.
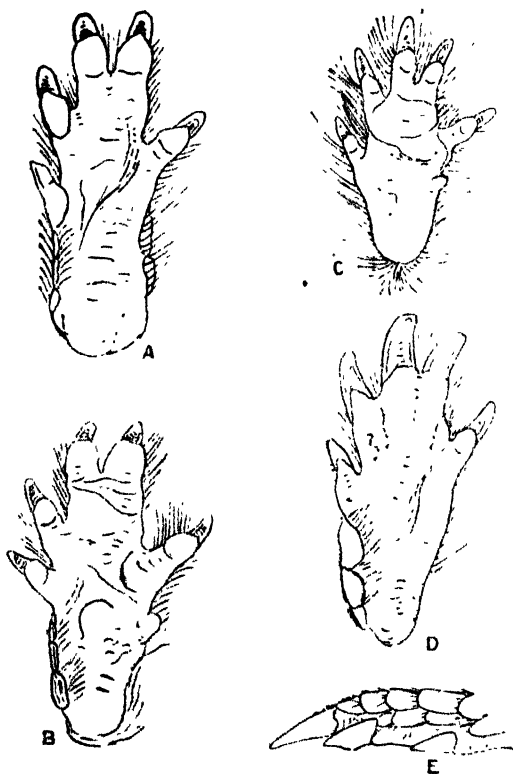
A. Right hind foot of *Euphractus sexcinctus* from below.

B. The same of *Euphractus villosus*.

C. The same of *Zaëdyus pichyi*.

D. The same of *Cabassous unicinctus* (from a dried skin).

E. Digits of the same from the outer side.

The *hind foot* is always pentadactyle, and the arrangement of the digits is typically the same as in the fore foot, but the claws are always shorter and usually blunter and less unequal in length,

being. for obvious reasons, less fossorial in function. In *Euphractus sexcinctus* the hind foot is longer than the fore foot, the 2nd and 3rd digits are the longest, subequal, and closely united

Text-figure 26.
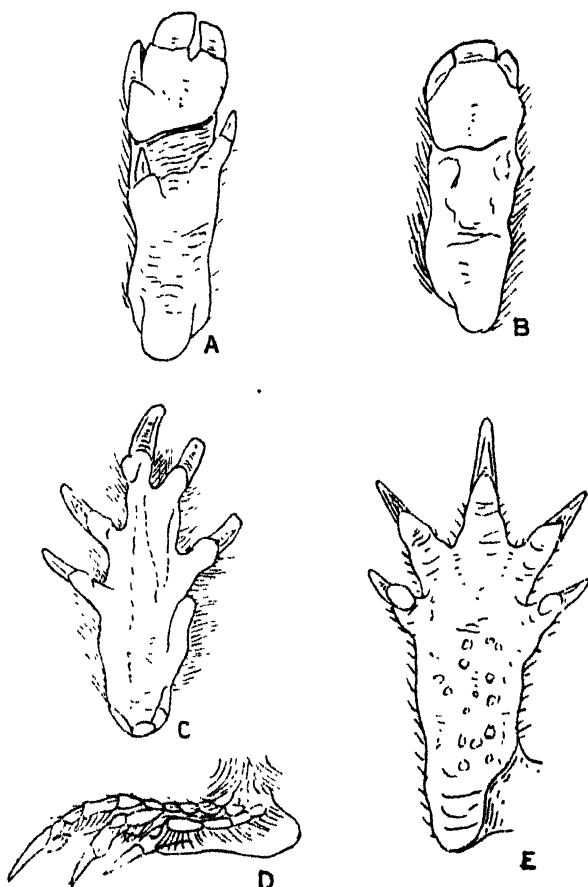
A. Right hind foot of *Tolypeutes mataca* from below.
B. The same of *T. muriei* (after Murie).
C. The same of *Chlamyphorus truncatus*.
D. The same from the outer side.
E. The same of *Dasypus novemcinctus* from below.

down to the proximal end of the ill-defined pads. The 4th is similar to them but set considerably higher up the foot. The 5th, too, is similar but smaller and less prominent, and is a little farther

from the 4th than the latter is from the 3rd. The 1st, set a little above the level of the 4th, but below the 5th, is much longer than the 5th and more movable and capable of being folded across the sole, which is naked, wrinkled, and without pads. There is a fringe of hair on the inner side of the foot and scattered hairs on its outer side and in the interdigital spaces. In *Eu. villosus* the foot is somewhat shorter and carries a tubercular excrescence on the inner side behind the 1st digit, which is larger. (Text-fig. 25, A, B.)

In *Zaëdyus minutus* the hind foot is similar to that of *Eu. villosus* but is relatively shorter, more hairy, and has the digits less fused and more movable. (Text-fig. 25, C.)

In *Cabassous unicinctus* the hind foot is generally similar to that of *Euphractus*, but the 2nd and 3rd digits are fused to the tip and the claw of the 3rd is markedly longer than that of the 2nd. (Text-fig. 25, C, D, E.)

In *Priodontes*, judging from mounted specimens, the hind foot is stout and compact, the digits, which are fused apparently even more thoroughly than in *Cabassous*, being armed with blunt hoof-like claws.

In *Chlamyphorus* the hind foot is formed on the same plan as that of *Euphractus*, but all the digits are less fused to the sole and the 3rd is markedly longer than the 2nd, carries a larger claw and shows a small pad-like swelling on its outer side at the base of the claw. On the inner side of the foot the posterior half of the sole is expanded behind the 1st digit. This expansion recalls the tubercle occupying the same position in *Eu. villosus* and *Zaëdyus*. (Text-fig. 26, C, D.)

In *Dasypus* the hind foot differs from those already described in being larger than the fore foot and subsymmetrically pentadactyle, the 3rd digit being median and noticeably longer and thicker than the 2nd and 4th, which are subequal, evenly spaced from the 3rd, and set at the same level, while the 1st and 5th, the smallest of the series, are also subequal, the 5th being at most slightly higher up the foot than the 1st. (Text-fig. 26, E.)

In *Tolypeutes*, although the digits are arranged approximately as in *Euphractus*, the hind foot differs in having the 2nd, 3rd, and 4th digits fused, and covered beneath by a distinct horny pad, beyond the distal edge of which the claws project. This pad is sharply defined behind, and separated by a space of soft skin from a second, less well-defined, pad lying between and behind the 1st and 5th digits. The claws of these are short and sharp, but those of the 2nd, 3rd, and 4th are broad and nail-like. In walking and standing the foot rests upon the pad of the 2nd, 3rd, and 4th digits, the claws of which are functionless for digging. The 1st and 5th toes are raised high above the ground and are represented externally, mainly by their claws, which are longish and sharp in *T. tricinctus* and *T. mataca (conurus)*; but so small in *T. muriei* that the artist omitted them from the drawing of the type. (Text-fig. 26, A, B.)

b. *The Feet of the Anteaters.*

The *fore feet* of the three South American Anteaters—*Tamandua*, *Myrmecophaga*, and *Cyclopes* (*Cyclothurus*)—differ greatly from those of the Armadillos.

In *Tamandua*, the least specialised in this respect, the 5th digit is suppressed. Of the remaining four the 3rd is considerably longer and very much stouter than the 2nd or 4th and carries a huge, compressed, falcate claw. The 2nd and 4th, with similar but smaller claws, are subequal in size and set at equal distances on each side of the 3rd, the respective interdigital spaces being tolerably deep, much deeper than in any member of the Loricatæ. The 1st is much smaller than the 2nd and is attached by webbing to its outer side, so that the space between them is quite shallow. The under side of the digits and of the digital portion of the sole is covered with soft, naked, wrinkled skin ; but above and behind this there is a great, thick, granular, cushion-like pad, which on the outer side of the foot is especially well developed and extends up to the base of the 4th digit, whereas on the inner side it is much shorter.

Tamandua is an active climber, although not by any means wholly arboreal ; and the digits are normally so strongly flexed as to be incapable of extension, admitting of the application of the lower sides to the ground in plantigrade progression. The tips of the claws and the proximal end of the great pad could alone be applied to the ground. Moreover, the alternative method of resting on the upper sides of the folded claws would injure the pad by forcing the tips of the great third claw into it. These considerations supply the clue to Tamandua's method of placing the outer side of the fore foot on the ground and resting upon the pad and 4th digit. In adaptation to that method the pad is especially well developed on the outer side of the sole and the corresponding surface of the 4th digit is naked. The posterior portion of the pad is used for grasping branches when the great claw of the 3rd digit is folded back over the sole. (Text-fig. 27, A, B, C, D.)

The fore foot of *Myrmecophaga* is clearly derivable from that of *Tamandua*, but very different from it. Its specialisations are subservient to terrestrial walking and digging, not to climbing. As in *Tamandua* the 5th digit is aborted, and the 1st is the smallest, but the latter is set higher up the inner side of the foot than in *Tamandua* and is disconnected from the 2nd. The 2nd is stout, as stout as the 3rd but not so long, and the two are separated by a moderately deep and wide space; its claw is nearly as long as that of the 3rd. The 4th has quite a small claw and is separated from the 3rd by a tolerably wide but shallow space. Behind its base there is a great, almost hemispherical, cushion-like, roughened, hairless pad, which forms a prominent bulge on the outer side of the foot. The rest of the sole is covered with soft hairless skin, and above the sole there is an isolated, median, transversely reniform, granular, carpal pad.

Apart from the comparatively less important differences in the size and disposition of the digits, the chief differences between the fore foot of *Tamandua* and *Myrmecophaga* are as follows:— *Tamandua* rests practically the whole of the outer side of the fore foot, from the tip of the 4th digit to the carpus, on the ground, the pad forming a continuous cushion along the outer side of the

Text-figure 27.
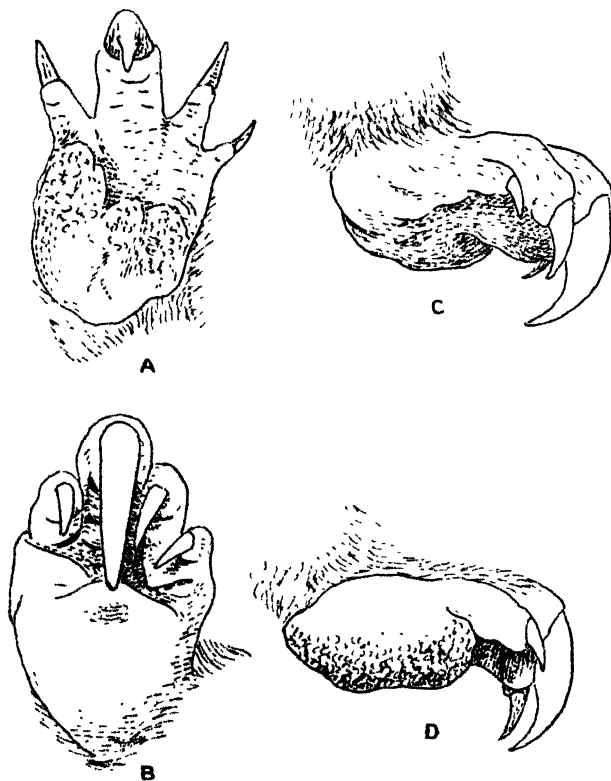
A. Right fore foot of *Tamandua tetradactyla* from below, with the digits spread.
B. The same, with the digits flexed.
C. Left fore foot from the inner side, showing the method of planting the foot on the ground during progression.
D. Right fore foot from the outer side, showing the ambulatory pad.

sole. *Myrmecophaga* rests upon the outer side of the 4th digit and of the distal portion of the sole. The pad is not continuous along the outer side of the sole to the wrist, the carpal portion of the pad being isolated and raised high above the ground, the tip of the great claw, when folded on the sole, fitting into a shallow pit just below it. (Text-fig. 28, A, B, C.)

Text-figure 28.
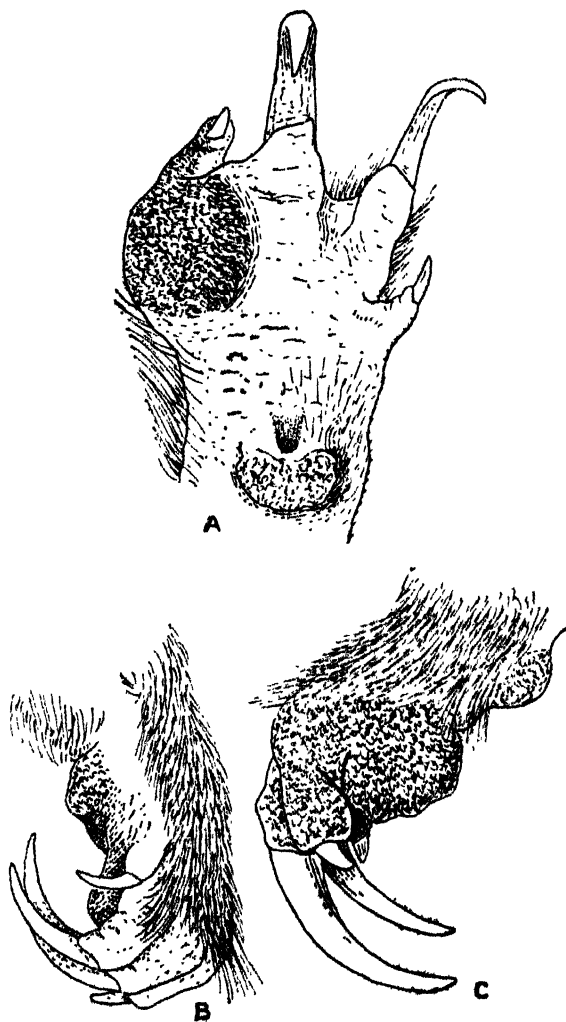
A. Right fore foot of *Myrmecophaga tridactyla* from below, showing the restriction of the ambulatory pad to the 4th digit, and the carpal pad raised from the ground.

B. Left fore foot from the inner side, showing the method of planting the foot during progression.

C. The same from the outer side.

The fore foot of *Cyclopes* (*Cyclothurus*) is also clearly derivable from that of *Tamandua*, but the structural modifications have taken the direction of almost complete subservience to climbing. Apart from the entire suppression of all external trace of the 1st and 4th digits, the 2nd and 3rd alone persisting, the foot is tolerably like that of *Tamandua*. The two digits are united by webbing almost to their distal ends, and are set nearly on a level. The 3rd

Text-figure 29.
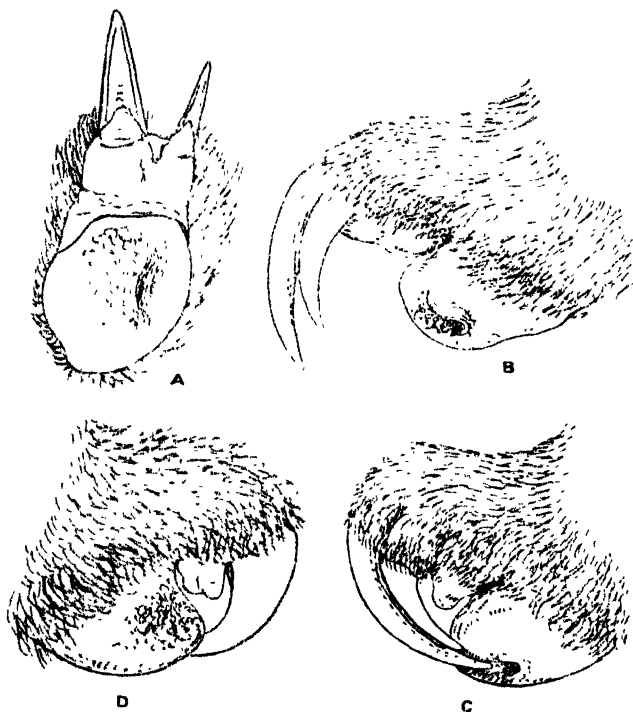
A. Right fore foot of *Cyclopes didactylus* from below, showing suppression of the 1st and 4th digits (the digits abnormally extended).

B. The same from the inner side, with the digits normally extended.

C. The same, with the digits flexed on the pad.

D. The same from the outer side.

is much stouter but not much longer than the 2nd, apart from its claw which, as in *Tamandua*, is very long, powerful, and falcate. The proximal portion of the under side of the foot is covered by a great, continuous, cushion-like, granular pad, which is thicker than that of *Tamandua*, but does not extend relatively so far forward along the inner side of the sole. The claw of the 3rd digit, when folded, presses upon the inner half of this pad, its

tip resting in a shallow depression. The pad and the claws of this foot constitute a powerful grasping instrument. (Text-fig. 29, A–D.)

The *hind feet* of *Tamandua* and *Myrmecophaga* are very similar to one another, but quite unlike those of the Armadillos. In

Text-figure 30.

A. Right hind foot of *Cyclopes didactylus* from below, with the digits abnormally spread, showing the joint in the sole.
B. The same from the outer side.
C. The same of *Tamandua tetradactyla* from below.
D. The same of *Myrmecophaga tridactyla*.

Tamandua there are five short digits, subequal and tolerably evenly spaced and set nearly in a line along the distal edge of the foot, the 1st being a little the shortest of the series. The claws are moderately long, curved and sharp for climbing. The sole, indistinctly divided into a proximal and distal portion, is about twice as long as broad. It is naked and moderately rough

and narrower at the heel, which is typically raised a little from the ground in walking. (Text-fig. 30, C.)

The foot of *Myrmecophaga* apparently differs from that of *Tamandua* in having the 1st digit relatively smaller and set a little higher above the 2nd, the claws shorter and blunter and in being a little less plantigrade, a larger area of the sole being raised from the ground in walking, the raised area of the heel being defined by a shallow integumental groove. (Text-fig. 30, D.)

The hind foot of *Cyclopes* is a modification of that of *Tamandua*. It is tetradactyle, the 1st digit being suppressed; the remaining four are fused almost up to their distal ends; the claws are longer and stronger, and the sole, which has a wide prominent heel, is covered with a pad which is granular in the centre behind, its anterior third behind the digits being sharply defined from the rest by a deep transverse groove of soft skin forming a joint, so that the claw-bearing part of the foot can be closed upon the rest of the sole and heel for grasping branches. (Text-fig. 30, A, B.)

c. *The Feet of the Sloths.*

The feet differ greatly from those of the Armadillos and Ant-eaters, even from those of *Cyclopes*, which they might perhaps be expected to resemble in adaptation to tolerably similar arboreal habits. Their greater perfection as climbing hooks is perhaps correlated with the absence of the prehensile tail found in *Cyclopes* and *Tamandua*. Owing to the great length and im-possibility of complete extension of the claws, Sloths apply the outer side of both fore and hind feet to the soil when moving on the ground.

The fore feet in the two genera, *Cholœpus* and *Bradypus*, differ in several features besides the well-known character of the reduction of the digits to two in the former and the retention of three in the latter. In *Bradypus* the digits retained are the 2nd, 3rd, and 4th; in *Cholœpus* the 2nd and 3rd, judging from the analogy of *Cyclopes*. They are nearly equal in length and are fused practically up to the base of the claws, which are long, compressed, pointed, and curved, and fold down upon the sole in a vertical plane.

In *Cholœpus* the foot is relatively much longer and narrower than that of *Bradypus* and is gradually narrowed distally. It is covered below by a continuous horny pad extending from the wrist to the base of the claws, where it passes into soft membrane, permitting the digits to be flexed. Laterally it is, to a slight extent, overlapped by the tips of the hairs of the sides of the foot. The sole which, apart from its wrinkles, is smooth, is nearly four times as long as wide, and the tips of the claws, when flexed, fall considerably short of its proximal end. (Text-fig. 31, E.)

In *Bradypus* the foot is relatively wider, owing mainly to the

Text-figure 31.
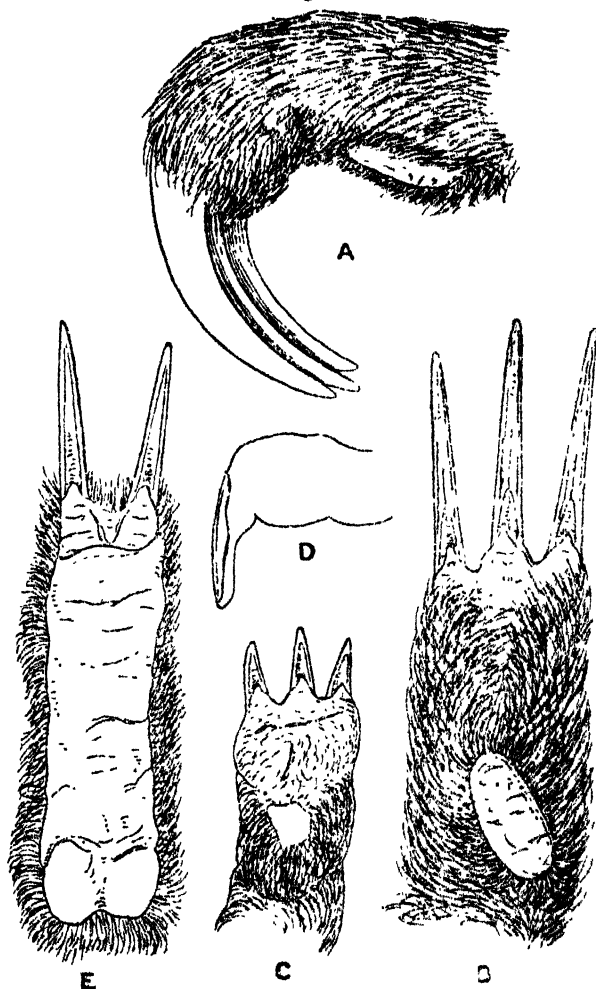
A. Right fore foot of *Bradypus tridactylus* from the inner side, with the
      hairs parted to reveal the pad.
B. The same from below, with digits abnormally spread.
C. The same of a young specimen.
D. The same of a fœtal young from the side, showing the extension of the
      digital pad to guard the tip of the claw.
E. The same of *Cholœpus*, showing the suppression of the 4th digit and the
      entirely naked sole when the hairs are turned aside.

retention of the 4th digit. The greater part of the sole is overgrown with hairs; but at its proximal end there is a large, elongated pad, about twice as long as wide, with rounded anterior and posterior extremities. It lies obliquely across the middle line, the greater part of it being on the inner side of the sole. Normally this pad is completely overlapped and concealed by the long hairs of the sole, which are directed inwards towards the middle line. The claws are relatively longer than in *Cholœpus* although the sole is shorter. Hence the tips of the claws, when flexed, overlap the proximal end of the pad above described. (Text-fig. 31, A, B.)

The *hind feet*, which in both genera are three-toed, have a very pronounced calcareal prominence, and the claws, instead of closing longitudinally upon the sole, close somewhat obliquely, so that the tips lie towards the inner side.

They differ in the two genera similarly to the fore feet, the sole in *Cholœpus* being quite naked, whereas in *Bradypus* it is mostly overgrown with hair except posteriorly, where there is an elongated pad lying along the underside of the heel, and this pad, as in the case of the fore foot, is naturally entirely concealed beneath the long, inwardly directed hairs of the sides of the heel. When the claws of the hind foot are flexed, their tips just reach the distal or anterior end of this pad. (Text-fig. 32, A, B, E.)

The feet of the newly born young of *Bradypus* show some interesting variations from those of the adult. The claws are comparatively short; so also is the hair, the soles, as in *Cholœpus*, being uncovered by the hairs clothing the sides of the foot. The fore part of the sole behind the claws, consisting of a cushion-like pad of skin, is rather sparsely covered with short pale hairs, which in the fore foot extend posteriorly to the horny pad, an irregularly triangular patch lying near the centre of the posterior half of the sole. It is noticeable that this pad is situated considerably in front of the wrist. (Text-fig. 31, C.)

In the hind foot the anterior cushion-like pad is sharply defined by a transverse crease from the posterior horny pad, which is relatively much longer than in the adult and runs backwards, gradually narrowing in its course, to the tip of the heel, covering about two-thirds of the surface of the sole. Since its anterior end coincides with the joint between the metatarsus and the digital phalanges, this pad may be regarded as representing the fused plantar and metatarsal pads of the normal mammalian foot.

Similarly, in the case of the fore foot, the position of the pad, far in advance of the carpus, suggests that it is the remnant of the plantar pad, the anterior cushion in both cases representing apparently the fused digital pads.

The features presented by the sole of the foot in the young of *Bradypus* confirms the inference, derivable from the nakedness of the sole in other Edentates, that its hairiness in the adult is a specialised, not a primitive, character.

Text-figure 32.
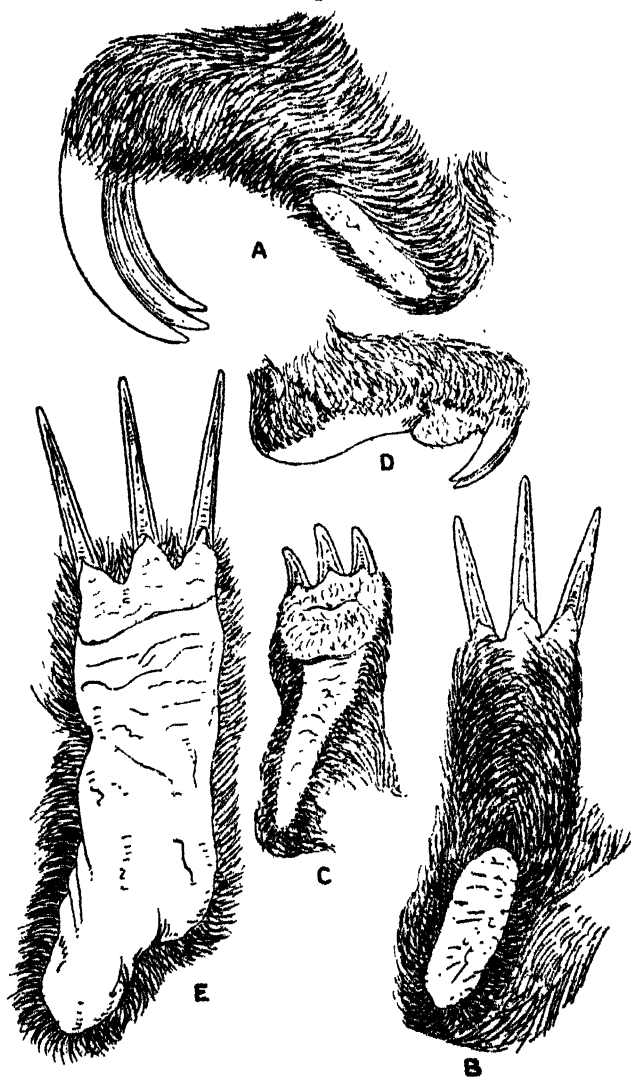
A. Right hind foot of *Bradypus tridactylus* from the inner side, with the hairs parted to reveal the pad.

B. The same from below, the digits abnormally extended.

C. The same of a young specimen.

D. The same from the outer side.

E. The same of *Cholopus*, showing the entirely naked sole when the marginal hairs are turned aside.

The principal variation in the structure of the feet in the Edentates may be summarised as follows:—

a. Fore and hind feet approximately similar in form, long and narrow, the digits fused, subequal, armed with long subequal claws . . . .   SLOTHS.
   b. Soles of feet entirely naked back to carpus and heel; two toes on fore foot   ... .   *Cholœpus.*
   b'. Soles of feet mostly overgrown with long hairs, but provided proximally with a flat horny pad, normally concealed by overlapping hairs; three toes on fore foot   .   *Bradypus, Scœopus.*
a'. Fore and hind feet dissimilar; fore foot with the digits unequal in size.
   c. 3rd digit of fore foot much larger than 2nd and armed with a longer falcate claw: digits of hind foot set approximately in a transverse line, alike and subequal   ANTEATERS.
      d. Fore foot with two digits only, the 1st and 4th suppressed; no great ambulatory pad on its outer side but a great cushion-like scansorial pad on the proximal portion of the sole; hind foot with four digits fused to their proximal ends and armed with long scansorial claws, the sole very distinctly jointed and with a broad rounded heel   *Cyclopes.*
      d'. Fore foot with four digits, an ambulatory pad on the outer side behind the 4th digit; hind foot with five short separated digits armed with shorter claws, sole not distinctly divided by a joint, the heel narrowed.
      e. The sole of the fore foot covered externally and posteriorly with a continuous scansorial and ambulatory pad .   *Tamandua.*
      e'. Sole of fore foot with very large external ambulatory distal pad, the rest covered with soft skin with a small isolated reniform carpal pad   . . . .   *Myrmecophaga.*
   c'. 3rd digit of fore foot, excluding its claw, generally considerably shorter than 2nd, rarely slightly longer (*Dasypus*); digits of hind foot unequal, never in a transverse line, at least the 1st and 5th set higher than the rest   ARMADILLOS.
      f. Digits 2, 3, and 4 of hind foot completely fused, their claws hoof-like and the skin of their under sides forming a thick ambulatory pad, digits 1 and 5 remote from them and supplied with normal claws; fore feet supported on tips of claws of digits 2 and 3 .   . . . .   *Tolypeutes.*
      f'. Digits 2, 3, and 4 of hind foot never fused into a compact mass with three hoof-like claws and a pad beneath, the claws of all the digits alike and fossorial; fore foot plantigrade.
      g. Fore foot with four digits, the 5th aborted; the 3rd never shorter but slightly longer than the 2nd; hind foot with digits 1 and 5, 2 and 4 subsymmetrically paired, the 3rd the longest and median   .   *Dasypus*
      g'. Fore foot with five digits, the 3rd, excluding its claw, shorter than the 2nd; hind foot with digits irregularly arranged, the 2nd and 3rd subsymmetrically paired, but the 1st above the 4th, the 5th above the 1st.
      h. Fore foot with 5th digit bearing a blade-like claw and supported beneath by a plantar outgrowth; a smaller plantar outgrowth on inner side of hind foot behind the 1st digit; no carpal vibrissæ. . . . .   *Chlamyphorus.*
      h'. Fore foot with 5th digit bearing a pointed claw, no plantar outgrowth beneath it; at most a rounded tubercle projecting behind the 1st digit of the hind foot; carpal vibrissæ present.
      j. Digits of fore and hind feet, except 2nd of the fore foot, fused to base of claws; claws of fore foot relatively larger ....   *Cabassous.*
      j'. All the digits distally separable; claws of fore foot smaller   ....   *Euphractus, Zaëdyus.*

THE TAIL.

The dermal armature of the tail in Armadillos was described above (p. 988). For the rest the tail in this family varies very considerably in length and typically tapers from the broad base to the apex. It is longest in *Dasypus*, in which the segmentation and development of the dermal armature reaches its highest expression. In *Euphractus* and its allies it is long or moderately long, varying specifically in that respect. In *Cabassous* and *Priodontes* it is also moderately long, but of typical form. In *Tolypeutes* it is comparatively rigid, quite short, with a very broad base, from which it tapers rapidly to the point. In these peculiar Armadillos it acts as a peg to prop the body as the animal squats on its hind-quarters when digging, and when the body is rolled it lies alongside the head, helping to fill the space between the free margin of the pelvic and thoracic plates. In *Chlamyphorus* the tail is moderately long and relatively slender, not wider at the base, and is distinguished by the expansion of its distal end into a plate or spatula, approximately oval in outline. This expansion, no doubt, acts as a prop during digging operations; but possibly it serves also as an instrument to sweep aside the loosened soil.

In the Anteaters the tail is always long, as long as the body or longer, and tapers from the thicker base to the end. In *Myrmecophaga* it is scaly and comparatively rigid and inflexible, and is characterised by the development on its dorsal and ventral surfaces of a great crest of long hair, the function of which is apparently to constitute a covering for the animal in repose when the tail is stretched sideways over the exposed right or left side of the body with the head and snout tucked down along the ventral surface.

In *Tamandua* and *Cyclopes* it is flexible and prehensile. In *Tamandua* it is covered for the most part with small epidermal scales interspersed with short hairs, long hairs like those of the hind-quarters merely extending for a short distance over the dorsal and lateral portions of its base. It is shorter than the head and body in this genus; but in *Cyclopes* it is longer than those two regions combined and is, in addition, covered almost throughout with short close-set silky hairs, approximately only its terminal third beneath showing a narrow strip of naked integument. In the structure of the tail the line of demarcation between the Armadillos and Anteaters is not so pronounced as might be expected, owing to the partial suppression of the scutes and scales in *Cabassous* and the presence of epidermal scales in *Tamandua* and *Myrmecophaga*.

In the Sloths the tail is either quite short or absent. In *Bradypus* and *Scæopus* it is retained as an anal covering, an inch or more in length and thickly beset with longish hairs; but in *Cholœpus* it is practically aborted and does not project perceptibly above the anal orifice.

By the characters of the tail described in the last section and above on p. 988 the principal genera of Edentates may be arranged as follows:—

a. Tail absent or very short, in the latter case functional merely as
    an anal and genital operculum .. ..   *SLOTHS.*
  b. Tail vestigial . . .. *Cholœpus.*
  b'. Tail short, thickly hairy .... *Bradypus, Scœopus.*
a'. Tail always present, long or short, and functional in a variety
    of ways.
  c. At least the base of the long tail thickly covered with hairs
    like those of the body ; no bony scutes . ... *ANTEATERS.*
    d. Tail comparatively rigid, not prehensile, with a dorsal and
        ventral fringe of long hairs . ... *Myrmecophaga.*
    d'. Tail flexible and prehensile, without fringes of long hairs.
      e. Base of tail with long hairs, the rest covered with short
         hairs and small scales . . .. *Tamandua.*
      e'. Tail uniformly covered with short hairs apart from a
         naked strip in the distal half beneath . . *Cyclopes.*
  c'. Tail typically nearly naked and covered with armature of
    scutes and scales ; when the scutes are degenerate the scales
    are comparatively few and scattered, and the base is not
    covered with longish hairs .... . . *ARMADILLOS.*
    f. End of nearly naked tail with spatulate expansion . *Chlamyphorus.*
    f'. Tail evenly attenuated from base to tip.
      g. Tail comparatively very short but thick and almost
        inflexible, its dorsal scutes forming upstanding bosses
        or tubercles . . . . . *Tolypeutes.*
      g'. Tail moderately or very long, its scutes flat or slightly
        convex.
        h. Its armature reduced to small, irregularly arranged,
          sometimes hardly perceptible scales . ... *Cabassous.*
        h'. Its armature of scutes and scales well developed.
        j. Scutes close-set, not arranged in definite rings
          jointed by arthrodial membrane . *Priodontes.*
        j'. Scutes at least in the basal portion arranged in
          definite rings united by arthrodial membrane.
          k. Rings in basal portion of tail consisting of one or
            two rows of scutes . . .. *Euphractus.*
          k'. Rings in basal portion consisting of three rows
            of scutes . . . *Dasypus.*

THE ANUS AND EXTERNAL GENITALIA.

By the external characters included under this heading the Edentates are tolerably sharply divisible into two groups—the Armadillos constituting one, the Anteaters and Sloths the other.

a. *Of the Armadillos.*

In both sexes the anus is exposed as a subcircular area above and distinct from the generative orifice. It is provided with a pair of large anal glands which in a fresh example of *Dasypus novemcinctus* were tolerably deep pockets, with folded walls invested in muscular tissue and containing a yellow nauseous secretion. (Text-fig. 35, A, C.)

In the female the genital orifice is closer to the anus, there being a shorter perineal area than in the male.

In *Dasypus* (*Tatusia*) the vulva is comparatively short and piriform or conical, the narrowed inferior portion which carries

the orifice being furnished with two dilatable labia. (Text-fig. 33, A, B.)

In *Zaëdyus minutus* the perineal area is longer than in *Dasypus*. The vulva has an expanded base which passes somewhat abruptly into a narrow elongated clitoris, at the base of which lies the short slit-like urino-genital orifice, the greater part of the clitoris being entire, without a median groove continuous with the orifice. (Text-fig. 33, E.)

Text-figure 33.
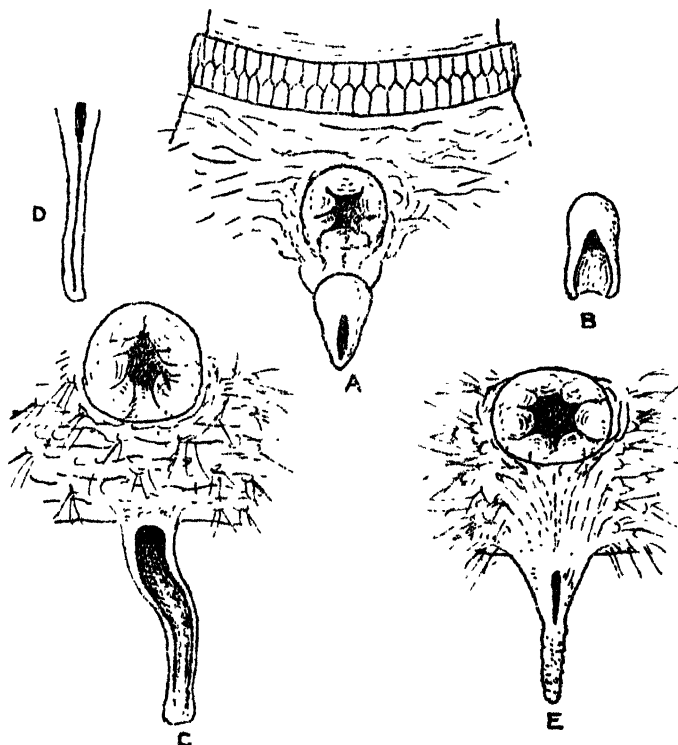
A. Vulva, anus, and base of tail of *Dasypus novemcinctus*.
B. Vulva of the same, with labia separated.
C. Anus and vulva, with long expanded clitoris, of *Euphractus sexcinctus*.
D. Vulva and clitoris of the same, with the gutter closed.
E. Anus and vulva with ungrooved clitoris of *Zaëdyus pichyi*.

In *Euphractus sexcinctus* the perineal area is as long as in *Zaëdyus*, but the clitoris is relatively longer and penis-like. It shows no definite basal expansion, but is of tolerably even thickness throughout and exhibits a gutter-like dilatable groove running from the base, where the urino-genital orifice is situated, to the apex. (Text-fig. 33, C, D.)

According to Garrod the clitoris in *Cabassous* (*Xenurus*) and *Tolypeutes* agrees in relative size with that of *Euphractus*. On the other hand, the external genitalia of the female of *Chlamyphorus* are described as small.

Text-figure 34.
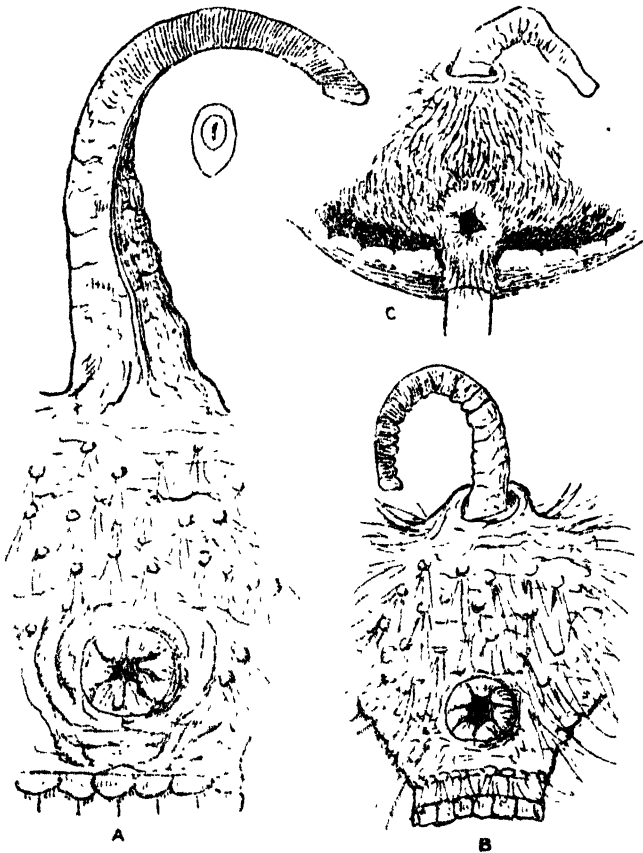
A. Penis, anus, and base of tail of *Euphractus sexcinctus*.
B. The same of *Zaëdyus pichyi* (*Euphractus minutus*).
C. The same of *Chlamyphorus truncatus*, showing also the freedom of the thighs from the pelvic carapace.

Setting *Chlamyphorus* aside, it will be seen from the above-given account that in its external genitalia *Dasypus* (*Tatusia*) differs considerably from *Euphractus*, *Cabassous*, and *Tolypeutes**.

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* It may also be noted, as pointed out by Garrod, that *Dasypus* (*Tatusia*) further differs from those three genera in having a piriform instead of a triangular uterus That organ is also piriform in *Chlamyphorus*.

Text-figure 35.
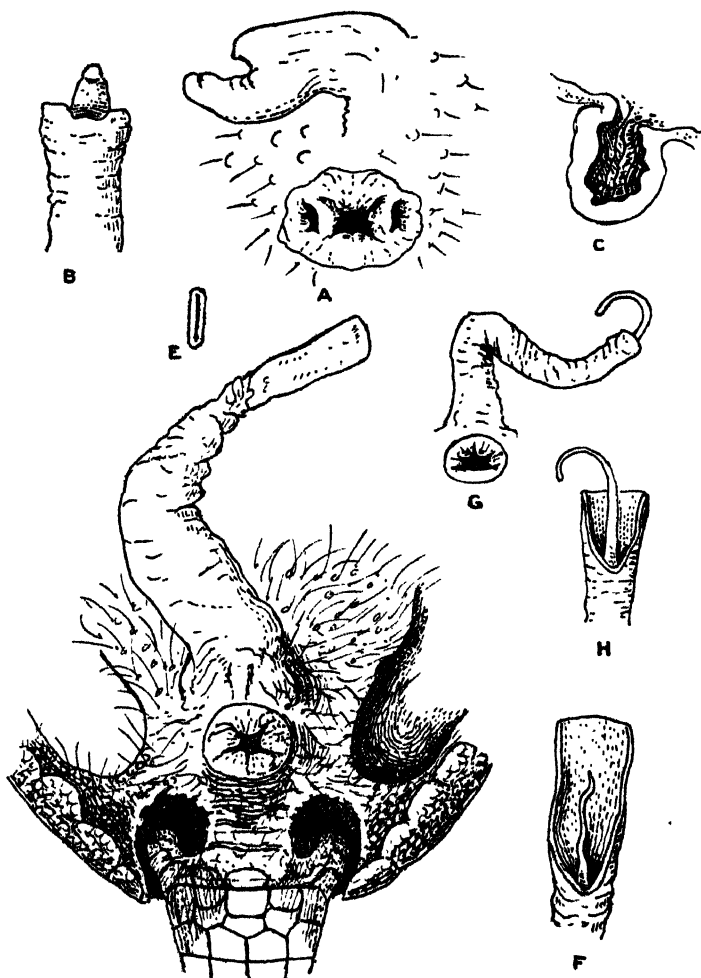
A. Anus and penis of *Dasypus* (*Tatusia*) *novemcinctus*. The anus is spread to
    show the orifices of the anal glands, and the penis is turned towards the
    animal's right side and seen from the side.
B. Distal end of penis of the same from above.
C. Section of anal gland of the same.
D. Penis, anus, and base of tail of *Tolypeutes mataca* (*conurus*), showing also
    the basal joint of the tail, and on the animal's left the posterior portion
    of the cavity which lodges the hind leg.
E. Orifice in tip of penis of the same.
F. Sheath of distal end of penis of the same cut open to show the concealed
    filiform apex.
G. Anus and penis of newly-born young of *Tolypeutes* sp.
H. Sheath of distal end of penis of the same cut open to show the partly
    concealed apex.

In male Armadillos there is no scrotum and the perineal area is short or very long; the penis is always large and pendulous, but differs considerably in structure in some of the genera. In *Dasypus* (*Tatusia*) it is comparatively short and thick and nearer to the anus. Its extreme apex is simple with a terminal orifice; but just behind and above the narrower terminal portion it is expanded into a pair of rounded lobes. Garrod correctly described it as apically trilobed. It seems clear from its structure that only the narrower terminal portion carrying the orifice enters the vulva during copulation. (Text-fig. 35, A, B.)

In the genera *Euphractus*, *Zaidyus*, *Cabassous*, and *Chlamyphorus*, according to my observations and those of others, the penis is very long, almost vermiform, gradually but not greatly attenuated distally, transversely grooved and ridged and, in repose, curved or bent, the orifice being small and terminal. (Text-fig. 34, A, B, C.)

No great difference, so far as I am aware, has hitherto been detected between the penis of *Tolypeutes* and those already described. Murie's figure and description of the organ in *T. muriei** suggest this similarity. But in an adult male of *T. mataca* (*conurus*) I find a profound difference. The penis, which emerges a short distance in front of the anus, the perineal area being short, is very long and very stout in its basal two-thirds, the distal third, which carries a slit-like terminal orifice, forming a compressed blade-like portion, somewhat rounded and defined by a shallow constriction at the base. The orifice above mentioned is not the urino-genital orifice, but the orifice of a sheath which acts as a protective covering for the true termination of the penis, which is exceedingly slender, filiform, and pointed, and normally entirely concealed from view within the sheath above described. (Text-fig. 35, D, E, F.)

In a newly born example of the same or an allied species of *Tolypeutes*, the terminal fourth of the penis is abruptly narrowed, slender, and coiled; and the base of this slender portion is insunk into the adjacent portion of the penis which encircles it like a collar. Possibly this penis would have altered with growth so as to resemble that of the adult *T. mataca*. (Text-fig. 35, G, H.)

By the characters of the external genital organs the genera of Armadillos may be arranged as follows :—

a. Vulva short and piriform ; penis comparatively short and stout
    with bilobed excrescence above the narrower terminal portion . *Dasypus.*
a'. Vulva with elongated slender clitoris (? in *Chlamyphorus*);
    penis very long, without excrescence above terminal portion.
b. Terminal portion of penis slender and in adult ensheathed
    within the adjacent end of the proximal portion   .   . *Tolypeutes.*
b'. Terminal portion of penis not sheathed and not differentiated
    from the rest ... .   *Chlamyphorus, Euphractus, Zaëdyus, Cabassous.*

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* Murie evidently did not cut open the end of the penis in his specimen.

Text-figure 36.
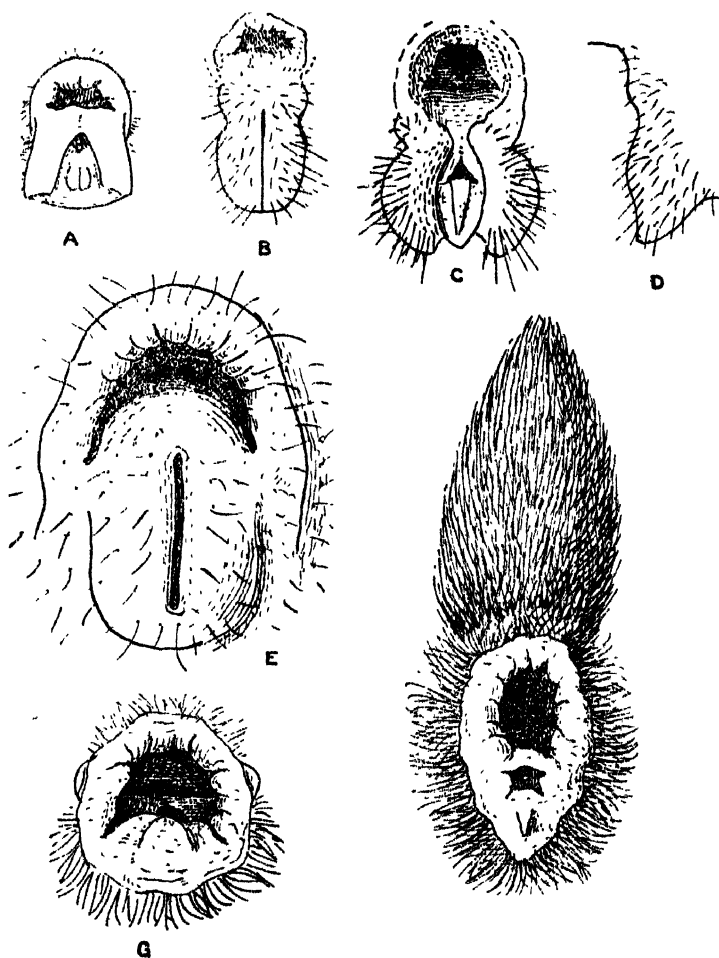
A. Anus and vulva, dilated, of *Cyclopes didactylus*.

B. Anal sac and vulva, with labia closed, of *Tamandua tetradactylus*.

C. The same, with the sac and labia spread.

D. The same from the side, showing the similarity to the similar organs of the male (text-fig. 37, A).

E. Anal and genital area of female *Myrmecophaga tridactyla*, showing the crescentic anal sac and the vulva beneath it.

F. Anal and genital area of female *Bradypus tridactylus*, vertically stretched by raising the tail.

G. The same partially closed, showing also portions of the anal glands.

b. *Of the Anteaters and Sloths.*

The Anteaters and Sloths differ from the Armadillos in having the anus and external genitalia close together, forming sometimes a common ano-genital eminence or situated on a common naked or nearly naked area of integument, the edges of which fold over them. The penis is always quite short, inconspicuous, and never abdominal, the sexes being difficult to determine without critical examination.

Text-figure 37.
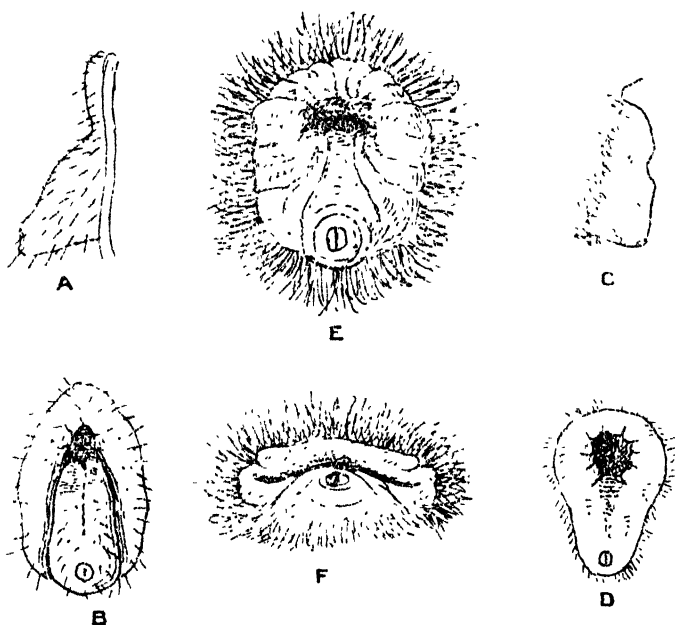
A. Side view of the anal and genital area of a male *Tamandua tetradactyla*.
B. Posterior view of the same, showing the penis just below the anus.
C. Side view of anal and genital area of a young male of *Cyclopes didactylus*.
D. Posterior view of the same.
E. Posterior view of the extended anal and genital area of half-grown male example of *Cholœpus*.
F. The same when closed.

In a female *Myrmecophaga* the anal orifice was sunk in an integumental sac, the orifice of which was a wide crescentically curved transverse slit with the concavity looking downwards. Beneath this was the long vertical cleft of the vulva bounded by a pair of thick labia, scantily hairy like the rim of the anal sac. (Text-fig. 36, E.)

In a young female *Tamandua* the anus is a large insunk aperture in the centre of a subcircular area of naked skin, and the

vulva beneath it, containing a simple undivided clitoris, is covered by a pair of thick hairy valvular labia. *Cyclopes* is similar to *Tamandua*, one specimen showing a distinct bilobed clitoris. (Text-fig. 36, A, B, C, D.)

In a male *Tamandua* the sheath of the short penis, with a small preputial orifice at the end, projects as a conical eminence immediately beneath the anus. A similar condition prevails in *Cyclopes*. (Text-fig. 37, A, B, C, D.)

The Sloths depart still more from the Armadillo type.

In a female *Bradypus tridactylus* the anus and vulva are situated close together on a common area of dilatable naked skin, which closes over them like a sac. The vulva has no definite labia and the clitoris is a small, ungrooved, simple process beneath it. But in a young example of apparently the same species the clitoris is distinctly grooved. (Text-fig. 36, F, G.)

In a male *Cholœpus didactylus* the anus and penis are similarly placed on an area of naked, radially wrinkled skin forming a common sac. The penis, a little distance below the anus, consists of little more than a small bilobate glans, surrounded by a circular preputial rim of skin at the lower end of the naked area of skin, the structure and arrangement of the whole area recalling that of *Tamandua*. The sac above described is closed by the downward folding of its upper portion over the anus and the upward folding of its lower portion carrying the penis with it. (Text-fig. 37, E, F.)

CONCLUSION.

Many attempts have been made to express the affinities of the Edentates systematically.

To Gray and, following him, to Huxley the peculiarities of the Sloths appealed sufficiently strongly to warrant their relegation to a group equivalent to the rest, although the rest comprised the Pangolins (*Manis*) and Aard Varks (*Orycteropus*), and, in the catalogue of Gray, *Echidna*, as well as the Anteaters and Armadillos. But whether *Manis* and *Orycteropus* be included or not in the order, it is nowadays conceded that they stand apart from the South American forms, which together constitute a natural assemblage. In the case of *Manis* and *Orycteropus*, the course followed by Weber of giving them independent ordinal rank as Squamata and Tubulidentata respectively appears to be correct, and I do not propose to consider them further in this connection.

With regard to the South American forms, to which the term Edentata is restricted, with Xenarthra as an alternative and perhaps preferable title, Flower's view that the Sloths and Anteaters should be affiliated and contrasted with the Armadillos is usually, if not invariably, adopted with or without comparatively unimportant amplifications or suppressions of titles of superfamilial or supergeneric value.

Flower's arrangement in 1891 was as follows :—

Suborder 1. Pilosa for the Bradypodidæ and Myrmecophagidæ *.
  „   2. Loricata for the Dasypodidæ.

So far as recent forms are concerned, Pilosa and Loricata are tolerably appropriate terms; but some of the Armadillos (e. g., *Dasypus* (*Cryptophractus*) *pilosus*) are richly provided with hair; and dermal scutes were present in some of the extinct ground-sloths. Considerations such as these probably influenced Max Weber in 1904 and Winge in 1923 † to drop these terms altogether, and induced Ameghino to substitute Anicanodonta and Hicanodonta for them respectively. Osborne, however, in 1910 (' Age of Mammals ') retained the titles Pilosa and Loricata, with Ameghino's terms as alternatives, but he divided the Pilosa into Tardigrada for the Sloths or Bradypodidæ and the Vermilingua for the Anteaters or Myrmecophagidæ.

Apart from the dermal covering, the external characters described in the foregoing pages furnish, with one exception, no evidence of closer kinship between the Sloths and the Anteaters than between either of those groups and the Armadillos. The exception is supplied by the external genitalia, more particularly of the male. The structure of these organs alone justifies the association of the Sloths and Anteaters in a primary subdivision of the Edentates equivalent to a second division containing the Armadillos. For these divisions the old names Pilosa (Anicanodonta) and Loricata (Hicanodonta) may be retained. But since the distinction between the Sloths and Anteaters surpasses the value of the characters upon which families of mammals are usually established, I propose to follow Osborne in admitting the titles Tardigrada and Vermilingua for the Sloths and Anteaters respectively.

These two groups may be considered first :—

TARDIGRADA. The three genera of Sloths— *Cholœpus*, *Bradypus*, and *Scœopus*—have always been referred to one family, the Bradypodidæ. But it is quite clear that they fall into two sharply-defined groups represented by *Cholœpus* and *Bradypus* + *Scœopus* respectively. The importance of the differences between the former and the two latter genera is entirely obscured by giving them generic importance only. The differences supplied by the hairy covering, the ears, the tail, and the feet described above, quite apart from the differences in the skulls and other points, appear to me to be quite sufficient to form the basis for two families, the Cholœpidæ for *Cholœpus* and the Bradypodidæ for *Bradypus* and *Scœopus*.

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* Here and elsewhere I omit from the classification the extinct ground-sloths (*Megatherium*, *Megalonyx*, etc.), which are admittedly related both to the Myrmecophagidæ and Bradypodidæ.

† This, the most recent classification of the order, which I shall refer to under the subordinate headings, may be found in Winge's Pattedyr-Slægter, i. pp. 274-353 (1923).

VERMILINGUA. The three genera *Cyclopes*, *Tamandua*, and *Myrmecophaga* are always assigned to a single family, Myrmecophagidæ. Winge, however. went to the extent of referring *Cyclopes*, which he called *Cycloturus*, to the sub-family Cycloturini, keeping *Tamandua* and *Myrmecophaga* in the subfamily Myrmecophagini. I 'propose to go a step farther than Winge and raise his subfamilies to the rank of families under the names Cyclopedidæ and Myrmecophagidæ, dividing the latter into two subfamilies, Tamanduinæ and Myrmecophaginæ, to emphasise the differences in structure and habits between these two Anteaters.

LORICATA. This is a more difficult group, with many genera.

Most of the writers of text-books admit one family of Armadillos, the Dasypodidæ, which is divided into three subfamilies—Dasypodinæ, Tatusiinæ, and Chlamydophorinæ, *Tolypeutes* being regarded as an -aberrant member of the Dasypodinæ. Winge referred all the existing Armadillos to a single subfamily; but since his grouping of the genera is novel and interesting I give it in full :—

$$
\text{I.}
\begin{cases}
\text{1. Euphracti.} & \textit{Euphractus} \text{ (formerly } \textit{Dasypus}).\\[1ex]
\text{2. Xenuri}
\begin{cases}
a.
\begin{cases}
a. & \begin{cases} \textit{Xenurus} \; (= \textit{Cabassous}).\\ \textit{Priodontes} \text{ (quoted as } \textit{Cheloniscus}).\\ \beta. \; \textit{Tolypeutes}.\end{cases}\\
b. & \textit{Chlamyphorus}.
\end{cases}
\end{cases}\\[1ex]
\text{II. 3. Dasypodes.} & \textit{Dasypus} \text{ (formerly } \textit{Tatusia}).
\end{cases}
$$

From this classification it appears that in Winge's opinion *Chlamyphorus* is more nearly akin to *Cabassous* (*Xenurus*) than the latter is to the typical Armadillos, *Euphractus*. Except that *Tolypeutes* is given higher rank, this classification resembles in essentials that of Flower, Weber, and others. It appears to me, however, that *Tolypeutes* in the structure of the shell, the feet, the male genitalia, and other characters is too specialised for inclusion in the Euphractidæ, containing more generalised types like *Euphractus* and *Cabassous*.

It seems needless in this summary to repeat all the characters of the genera already printed in the preceding pages. All that remains to be done is to give the proposed classification of the Edentates in tabular form.

Edentata or **Xenarthra.**

Subord. **Pilosa** (Anicanodonta).

TARDIGRADA.

Fam. CHOLŒPIDÆ (*Cholœpus*).

„ BRADYPODIDÆ (*Bradypus*, *Scœopus*).

VERMILINGUA.

 Fam. CYCLOPEDIDÆ (*Cyclopes*).

  „ MYRMECOPHAGIDÆ.

   Subfam. Myrmecophaginæ (*Myrmecophaga*).

    „ Tamanduinæ (*Tamandua*).

Subord. **Loricata** (Hicanodonta).

 Fam. DASYPODIDÆ (*Dasypus*).

  „ EUPHRACTIDÆ.

   Subfam. Euphractinæ (*Euphractus*).

    „ Cabassoinæ (*Cabassous, Priodontes*).

  „ TOLYPEUTIDÆ (*Tolypeutes*).

  „ CHLAMYPHORIDÆ (*Chlamyphorus*).

A REVISION OF THE SPONGE FAMILY DONATIIDAE.
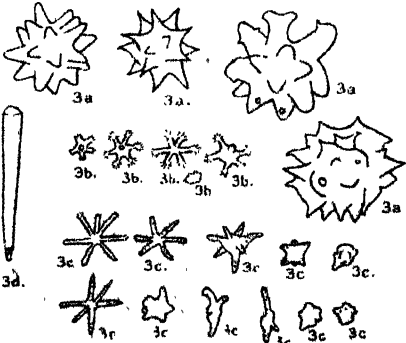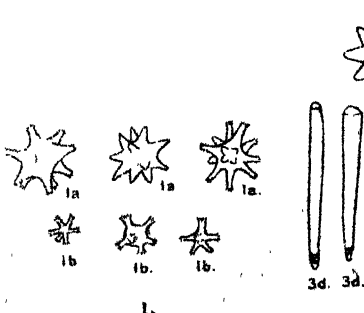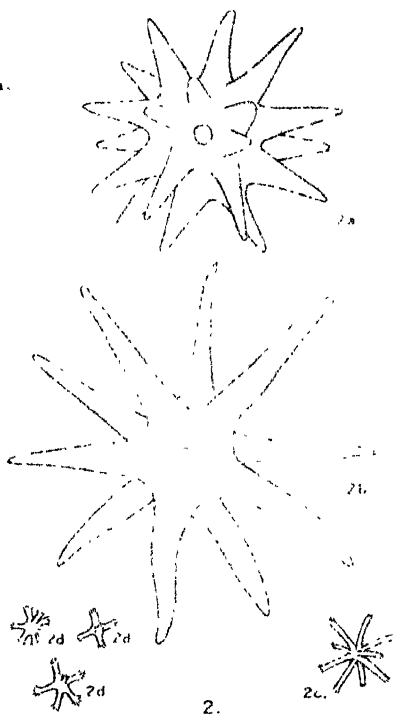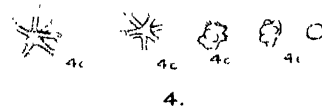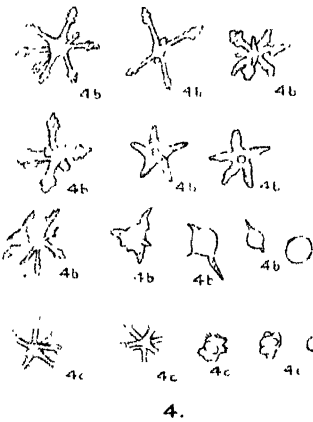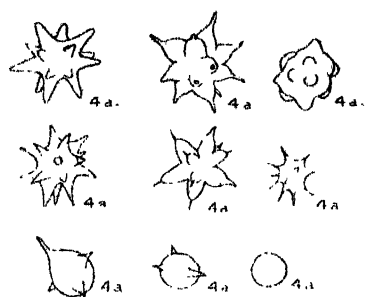
43. A Revision of the Sponge Family *Donatiidæ*. By
MAURICE BURTON, M.Sc., Research Student of King's
College, University of London[*].

(Plate I.)

In attempting a survey of the family Donatiidæ, the main
interest is of necessity centred upon the genus *Donatia*, which,
together with three monotypic genera (*Tethyorrhaphis*, *Xeno-
spongia*, and *Halicometes*), comprises the family as here understood.
The difficulties of defining the species of *Donatia*, and the great
need for a thorough revision of the genus, have been repeatedly
insisted upon by writers of recent years. Having had the good
fortune, through the kindness of Prof. A. Dendy and Mr. R.
Kirkpatrick, of being able to examine a large number of
authentic specimens, including many types, of *Donatia*, together
with a number hitherto unidentified, I feel in a position, as a
result of my observations, to propose an extensive revision of the
Donatiidæ and, in particular, of the genus *Donatia* itself.

Topsent (1918) carried out a very extensive survey of the genus
Donatia, and, as a result, made a number of very interesting and
valuable suggestions in regard to its revision. Handicapped by
the lack of type-specimens for examination, and the complete
inadequacy of the descriptions of Schmidt (1870 A), Bowerbank
(1873 A), and Lendenfeld (1888 A), his results were, in some cases,
inconclusive. With the re-examination of types it is now possible
to come to a definite decision regarding several species of which
only inadequate or inaccurate descriptions have hitherto been
available.

For the nomenclature of the family, I shall follow Dendy
(1916 c), and for the reasons he gives.

Family DONATIIDÆ.

(= TETHYADÆ or TETHIIDÆ auctorum.)

Diagnosis :—Astrotetraxonida without tetractinellid mega-
scleres. With strongly-developed fibrous cortex. Main skeleton
composed of radially-arranged monaxon megascleres. Micro-
scleres euasters of various kinds, always differentiated into
megasters and micrasters, to which microrhabds may be added.

[*] Communicated by Prof. ARTHUR DENDY, F.R.S., F.Z.S.

Genus 1. DONATIA Nardo (1833).

Synonymy :—*Alcyonium* Müller, O. F., 1779.
　　　　Tethya Lamarck, 1815 A.
　　　　Tethyum Lieberkuhn, 1859.
　　　　Anmiscos Gray, 1867 F.
　　　　Columnitis Schmidt, 1870 A.
　　　　Alemo Wright, 1881 A.

Diagnosis :—Donatiidæ of more or less spherical form ; megascleres strongyloxea ; megasters spherasters, typically cortical ; micrasters of various forms ; without microrhabds.

The genus *Donatia*, itself so singularly well-defined, contains a number of species which approximate so closely one to the other that their definition becomes a matter of almost insuperable difficulty, a fact which has been insisted upon by numerous writers, viz. :—Lindgren (1898 A), Dendy (1916 c), Topsent (1918), Wilson (1919). Nevertheless, in my opinion, it is possible to evolve a logical classification based mainly on the form of the micrasters, or smaller microscleres as opposed to the megasters ● large spherasters. The size and shape of the megascleres and megasters may occasionally be used, as in *D. repens* (Schmidt), *D. fissurata* (Lendenfeld), etc., although as a rule they do not show sufficient variation from one species to another to afford a basis for specific distinction.

The variations in the character of the cortex, used occasionally in the past as a means of separating one species from another, appears to be due to varying growth-phases, and has little significance for the systematist (*vide* Crozier, 1918).

The nature of the canal-system is difficult to determine in detail, but it appears to be diplodal and of a highly complex character. It is probable that in some cases several flagellate chambers may be supplied by a single branching aphodus, but of this it is impossible to be certain without the expenditure of a great deal of time on careful and minute investigation of specially preserved material, a thing impracticable at this juncture.

The colour is extremely variable (*vide* Crozier, 1918), and its significance obscure. In rare cases it may be due to symbiotic algæ (*vide* Dendy, 1905 A, and Baer, 1905 A). Only in one instance does it appear to be sufficiently constant to form a specific character, viz. : *D. magna*, in which the colour, purple-brown, is due to large pigment-cells very like those found in *Penares ochracea* (Carter). It may be possible that the "large red *Donatia* so common in the neighbourhood of Port Phillip, Victoria" (Dendy, 1916 c), may present a parallel case with *D. magna*, but, at present, this is doubtful, and the question could only be settled by careful observations of the sponge in the living state. Unfortunately, records of colour in the living state are all too few to admit of any definite generalisation.

By far the best known of the reproductive processes in *Donatia* is that by the formation of external buds (*vide* Sollas, 1888 B, and

Eichenauer, 1915).   Except for this, details of development are rare.   Both Sollas (1888 B) and Deszo (1878-1879) report the finding of embryos in the cortex in an advanced stage of segmentation.   From the work of the latter and Eichenauer (*l. c.*) it would appear that these embryos, "segmented ova or internal buds" of Sollas, are masses of amœbocytes, charged with nutritive material, wandering from the choanosome to take part, with outgrowths of the cortex, in the formation of buds, a purely asexual process.

I have already given a *résumé* of the sexual reproductive processes, so far as is known, in dealing with *D. magna* (*vide* Burton, 1924), which it would be unnecessary to repeat here.

The relationship of the various species of *Donatia* one to another presents some difficulty.   It is not difficult to trace a hypothetical phylogenetic relation between them, but how far this fits in with the true state of affairs it is hard to say.   Regarding the oxyaster as the most primitive micraster-form, *D. peracuata* is undoubtedly the most primitive species yet known.   Even in this, the rays of the micrasters are already becoming strongylote or tylote.   Near to it, and differing from it mainly in the almost complete absence of oxeote rays to the micrasters, are *D. lyncurium*, *D. repens*, *D. multistella*, and *D. deformis*.   From a form like *D. lyncurium*, by the differentiation of the micrasters into short-and long-rayed strongylasters, *D. robusta* and its allied species *D. magna* and *D. fissurata* have arisen.   In *D. diploderma* and the closely-related forms *D. maza* and *D. monstrosa* this differentiation of the micrasters has gone still further, giving rise to short-rayed tylasters and long-rayed oxyasters.   The probable derivation of *D. japonica* by the loss of the long-rayed oxyasters from forms like *D. diploderma* has already been suggested by Sollas (1888 B) and Lindgren (1898 A).

In conclusion, if the discussions of the various species appears at times too scanty, it is because they have already been fully dealt with by Topsent (1918), and for further details reference to his work should be made.

Species 1. DONATIA PERACUATA Topsent.

Synonymy :— × *D. lycurium* Dendy, 1916 c.
                 × *D. japonica* var. *peracuata* Topsent, 1918.

× signifies that the actual specimens described by the author quoted have been examined.

Diagnosis:—Micrasters oxyasters passing to strongylasters and, rarely, tylasters.

(For description and illustrations *vide* Dendy, 1916 c.)

Discussion :—I have already referred to the primitive character of this form and to the possible derivation of all the other known species from a form like it.

Distribution:—Salomon, Indian Ocean.

Species 2. DONATIA LYNCURIUM (Linnæus).

Type-species of the genus.

(For synonymy *vide* Lendenfeld, 1896 D, and Topsent, 1918.)

Diagnosis:—Micrasters typically strongylasters, but rays may be roughened and faintly tylote.

Discussion:—Lendenfeld (1896 D), in his list of synonyms of this species, has included Bowerbank's *Tethea ingalli*, *T. cliftoni* and *T. robusta*, and his own *Tethya corticata*. Omitting these, the list is a complete synonymy of *D. lyncurium*, and it is unnecessary to repeat it.

Distribution:—Atlantic coasts of Europe, Africa, North and Central America ; Mediterranean Sea.

Species 3. DONATIA REPENS (Schmidt).

Synonymy:— × *Tethya repens* Schmidt, 1870 A.

　　　　　　　× *Donatia fissurata* var. *extensa*, Hentschel, 1909 A.

　　　　　　　Donatia tylota Hentschel, 1912.

　　　　　　　× *Donatia stella-grandis* Dendy, 1916 C.

　　　　　　　Tethya fissurata Topsent, 1918.

Diagnosis:—Micrasters typically strongylasters with roughened rays, which may become tylote or occasionally oxeote ; rays of megasters long, often branched ; megascleres strongyloxea to tylostyli.

(For description and illustrations *vide* Dendy, 1916 C.)

Discussion:—Sollas (1888 B), in his examination of Schmidt's spicule-preparation of *T. repens* in the British Museum, appears to have paid no attention to the micrasters, the large size of the megasters, and the tylote ends of the megascleres. The preparation leaves much to be desired, but, on comparing it with Dendy's *D. stella-grandis*, I found them practically identical in size and form of spicule.

Hentschel's *D. tylota* and *D. fissurata* var. *extensa* are, on his own admission, hardly justifiably separated, and a comparison of his figures and descriptions with those of Dendy's *D. stella-grandis* leave little doubt as to the identity of all three with each other and with Schmidt's *D. repens*.

The species differ from *D. lyncurium* in the greater size of the megasters and the elongation and occasional branching of the rays, and by the development of tylote bases to the megascleres.

Distribution:—Florida (Schmidt); Shark's Bay, S.W. Australia; Arafura Sea (Hentschel); Amirante (Dendy); Maldives (Topsent).

Species 4. DONATIA DEFORMIS (Thiele).

Synonymy:—*Tethya deformis* Thiele, 1898 A.

　　　　　　　Tethya amamensis Thiele, 1898 A.

　　　　　　× *Tethya affinis* Kirkpatrick, 1900.

　　　　　　　Donatia papillosa Thiele, 1905 A.

　　　　　　　Donatia lyncurium var. *australis* Kirk., 1911.

　　　　　　× *Tethya stelloderma* Lendenfeld MSS.

Diagnosis:- -Micrasters typically strongylasters, rays of which may become tylote, usually with a more or less well-developed centrum; megasters small, usually not exceeding 0·04 mm. in diameter.

(For description and illustrations *vide* Thiele 1898, 1905, and Kirkpatrick 1900.)

Discussion: -Although very closely related to *D. lyncurium*, this species is distinguished from it by the complete absence of spines from the rays of the micrasters, a small enough character on which to base a specific distinction, it is true, and although it is here regarded as a distinct species, further research may prove it to be only a variety of the former.

Distribution:—Enoshima, Amami-Oshima, Japan (Thiele); Xmas Is. (Kirkpatrick); †New Zealand; †Tasmania; †Port Phillip Heads, Australia.

Species 5. DONATIA ROBUSTA (Bowerbank).

Synonymy:— × *Tethea robusta* Bowerbank, 1873 A.
　　　　　　× *Tethya globostellata* Lendenfeld, 1897 D.
　　　　　　× *Tethya ingalli* Kirkpatrick, 1900 A.
　　　　　　Donatia arabica Topsent, 1906 B.
　　　　　　Donatia japonica var. *albanensis* Hentschel, 1909 A.
　　　　　　× *Tethya lyncurium* Row, 1911.
　　　　　　× *Donatia ingalli* Dendy, 1916 C.
　　　　　　Donatia globostellata Topsent, 1918.
　　　　　　Donatia arabica Topsent, 1918.

Diagnosis: -Micrasters typically strongylasters of two kinds: (*a*) with short rays bearing at ends a number of small spines; (*b*) with long rays sometimes bearing a crown of small spines at the ends, sometimes sharply pointed—*i. e.* oxeote.

Discussion:—The true nature of *D. robusta* has for a long time been obscured. Ridley (1884 c) regarded it as a synonym of *D. lyncurium*, while Sollas (1888 B) placed it with *T. ingalli*. Topsent (1918) suggested the possible identity of *T. globostellata* Lendenfeld and his own *D. arabica* with *D. robusta*. This latter I have been able to confirm.

The species, while very closely related to *D. lyncurium*, differs from it in the greater differentiation of the micrasters, and in this respect occupies a position intermediate between it and *D. diploderma*.

Distribution:—†Australia; †New Zealand; †Indian Ocean; †Red Sea.

Species 6. DONATIA MAGNA (Kirkpatrick, 1903 B).

Diagnosis:—Micrasters strongylasters of two kinds, as in *D. robusta*; megasters do not form a dense cortical layer; stout

† Included in the distribution are hitherto unidentified specimens in the British Museum collection.

and extremely well-defined radial bundles of megascleres, with usually few loose spicules lying between them ; surface conulose ; pores in cribriform groups ; colour purple-brown.

Discussion :—At first I was inclined to regard this species merely as a variety of *D. robusta*, but examination of a dozen specimens sent over from South Africa by Dr. Gilchrist has prompted me to retain it as a distinct species. Although the spicules are so very like those of *D. robusta*, the absence of a dense cortical layer of megasters, so characteristic of the species of *Donatia* generally and of *D. robusta* in particular, the disposition of the megascleres, the large size of the specimens themselves, the colour (a purple-brown), and the peculiar character of the surface (*vide* Kirkpatrick, 1903 B, pl. i. fig. 6 *a*), seem points sufficiently distinctive to justify the retention of the species.

Although detail as to external form are lacking, the general characters and size of the spicules of Carter's (1882 A) specimen from the Cape seem to indicate that it belonged to this species.

Distribution :—Natal (Kirkpatrick); Cape Colony (Carter); Algoa Bay, Cape Point, South Africa (Burton).

Species 7. DONATIA FISSURATA (Lendenfeld, *non* Topsent). (Pl. I. fig. 2.)

Synonymy : — × *Tethya fissurata* Lendenfeld, 1888 A.
                    × *Tethya fissurata* Hallmann, 1914 A.

Diagnosis :—Micrasters strongylasters of two kinds : (*a*) with short rays bearing a number of small spines at ends (fig. 2 *d*) ; (*b*) with long rays bearing a few small spines at ends (fig. 2 *c*) ; megasters (figs. 2 *a* and *b*) incompletely differentiated into cortical and choanosomal.

(For description *vide* Hallmann, 1914 A.)

Discussion :—This species was originally inaccurately described by Lendenfeld, but has since been re-described by Hallmann. In the form of the micrasters i shows a striking resemblance to *D. magna*, from which species, and from all other species of *Donatia*, it differs, however, in the differentiation of the megasters and in the possession of a stout stalk.

Distribution :—Port Jackson, Australia (Lendenfeld); Storm Bay, Tasmania (Hallmann).

Species 8. DONATIA MULTISTELLA (Lendenfeld).

Synonymy :— × *Tethya mutistella* Lendenfeld, 1888 A.
                    × *Tethya multistella* Hallmann, 1914 A.

Diagnosis :—Micraster tylasters with outer ends of rays beset with small spines ; with or without centrum ; rays rarely oxeote.
(For description *vide* Hallmann, 1914 A.)

Discussion :—The close relationship of this species with a primitive form like *D. peracuata* is obvious. Hallmann (MSS.) regarded it as a variety of *D. lyncurium*, from which it is distinguished

chiefly by the pronouncedly tylote ends of the micrasters, and, although it is with considerable reluctance that I here retain it as a separate species, the difference in geographical distribution would appear to justify such action—as a provisional measure, at all events.

Distribution:—Port Jackson, Port Phillip, Australia (Lendenfeld, 1888 A and MSS.); Abrolhos Is., S.W. Australia (Dendy & Frederick, 1924).

Species 9. DONATIA JAPONICA (Sollas).

Synonymy:— × *Tethya japonica* Sollas, 1888 B.
　　　　　　Tethya japonica Lindgren, 1898 A.
　　　　　× *Tethya lyncurium* var. *a* Dendy, 1905 A.
　　　　　　Donatia japonica Topsent, 1906 B.
　　　　　× *Donatia japonica* Dendy, 1916 C.

Diagnosis: —Micrasters tylasters only, usually hexaradiate.
(For description of other features *vide* Sollas, 1888 B.)

Discussion:—The general characters and size of the spicules suggests the derivation of this species from *D. diploderma* by the loss of the long-rayed oxyasters. Moreover, it is no uncommon thing to find, in specimens of the latter species, a great sparsity of oxyasters, or even large tracts of the sponge from which they are entirely absent.

Distribution:—Manila; Java Seas; Ceylon; Indian Ocean; Red Sea.

Species 10. DONATIA DIPLODERMA (Schmidt).

Synonymy:— × *Tethya diploderma* Schmidt, 1870 A.
　　　　　× *Tethea ingalli* Bowerbank, 1873 A.
　　　　　× *Tethea cliftoni* Bowerbank, 1873 A.
　　　　　× *Alemo seychellensis* Wright, 1881.
　　　　　× *Donatia multifida* Carter, 1882 A.
　　　　　× *Tethya phillippensis* Lendenfeld, 1888 A.
　　　　　× *Tethya lævis* Lendenfeld, 1888 A.
　　　　　× *Tethya corticata* Lendenfeld, 1888 A.
　　　　　× *Tethya inflata* Lendenfeld, 1888 A.
　　　　　　Tethya maza Sollas (Miss), I. B. J., 1902.
　　　　　　Donatia viridis Baer, 1905 A.
　　　　　　Donatia parristella Baer, 1905 A.
　　　　　× *Donatia lyncurium* var. *c* Dendy, 1905 A.
　　　　　　Donatia ingalli var. *maxima* Hentschel, 1909 A.
　　　　　　Donatia japonica var. *globosa* Hentschel, 1909 A.
　　　　　　Donatia japonica var. *nucleata* Hentschel, 1909 A.
　　　　　× *Tethya ingalli* var. *lævis* Hallmann, 1914 A.
　　　　　　Donatia diploderma Topsent, 1918.

(For other possible synonymy *vide* Dendy, 1916 C, under *D. seychellensis*.)

Diagnosis:—Micrasters tylasters, often with ends of rays spined, and long-rayed oxyasters; rays of latter may be smooth, roughened, tuberculate or laterally spined, often branched, frequently hexaradiate.

(For descriptions and illustrations *vide* Dendy, 1916 c, and Topsent, 1918.)

Discussion:—The question of *D. diploderma* and its synonyms has already been discussed by Topsent (1918). Examination of Lendenfeld's *T. corticata* and *T. inflata* has shown them to belong to this species, and not to *D. japonica* as his descriptions might suggest (*vide* also Hallman, 1914 A).

Distribution:—† Indian Ocean ; † Australia ; † New Zealand ; † Malay Arch.; † Red Sea ; St. Thomas's Is., W. Africa ; † W. Indies ; † Bahia ; Acapulco, W. Mexico.

Species 11. DONATIA MAZA (Selenka).   (Pl. I. fig. 3.)

Synonymy:— × *Tethya maza* Selenka, 1879 A.
            × *Tethya maza* Sollas, 1888 B.

Diagnosis:—Micrasters tylasters (fig. 3 b) and long-rayed oxyasters (fig. 3 c); rays of latter, frequently reduced or almost entirely absent, often bluntly pointed, resembling in this condition strongylasters; megasters with variable rays (fig. 3 a); megascleres strongyloxea, which may become tylostyli or may, occasionally, be reduced to small forms measuring 0·45 by 0·036 mm. (fig. 3 d).

(For further description *vide* Sollas, 1888 B.)

Discussion :—Although obviously related to *D. diploderma*, the retention of *D. maza* as a separate species is justified by the abnormal form of its spicules. Undoubtedly originally derived from the species suggested above, *D. maza* appears to be, nevertheless, a well-established species, found in abundance, according to Selenka (1879 A), along the S. American coast between tide-marks.

Distribution :—Rio de Janeiro (Selenka); W. Indies (Eichenauer, 1915, p. 8).

Species 12. DONATIA MONSTROSA, sp. n.   (Pl. I. fig. 4.)

This species is represented by three nut-brown specimens of the usual spherical form in the British Museum collection labelled 47.12.30.17, and measuring from 14–25 mm. in diameter. The surface of each is subglabrous, with a very few small buds attached. The rooting processes are well-developed. No oscula are visible.

The megascleres are strongyloxea, which are arranged in radial bundles penetrating the cortex and spreading out in bushes beneath the surface. The spaces between the bundles are filled with loose radially-arranged megascleres.

Both cortex and choanosome are densely packed with micro-scleres exhibiting a remarkable series of abnormalities.

Spicules :—(1) Strongyloxea, of the size and form of those of *D. diploderma.*

(2) Spherasters (fig. 4 *a*), normally with large centrum and conical rays, but the latter may be reduced to domes bearing styliform processes at the apex, to domes only, to spines, or may disappear entirely, leaving a perfectly smooth sphere, 0·02 mm. in diameter. Diameter of the normal spheraster 0·048 mm.

(3) Tylasters (fig. 4 *c*), usually with centrum, 0·02 mm. in diameter. The rays may be reduced to knobs or may disappear entirely, leaving a smooth sphere.

(4) Oxyasters (fig. 4 *b*), with 6-12 rays, 0·032 mm. in diameter. The rays are normally more or less slender, but they may become tuberculate or thickened and rounded at the ends, with the development of a centrum at the junction of the rays. From this latter condition by the loss of the rays a perfectly smooth sphere is again formed.

This species, like *D. maza*, is closely related to *D. diploderma.* Distortion and reduction of the rays of the spherasters is by no means unknown among the Donatias, but whereas in most species the occurrence is rare, in *D. monstrosa* it is the fully-formed spicule which is seldom found. The nearest approach to this condition is found in *D. maza* and certain specimens of *D. diploderma* from Port Phillip Heads, Australia (Lendenfeld's *T. phillippensis, vide* Hallman, 1914 A). In the former the formation of spheres is confined to the micrasters, while in the latter they, together with other abnormal forms of spicules, occur only sparingly, and then only in a specimen here and there which, by other characters, cannot be logically separated from the other forms of *D. diploderma* so plentifully found in the same locality.

Distribution :—Tasmania.

Species dubiæ.

Tethya caudata Deszö, 1878-1879.

Tethea globum Duchassaing, P., et Michelotti, G., 1864.

Tethya ? innocens Schmidt, 1870 A.

Tethya nux Selenka, 1867 (*vide* Topsent, 1918).

I am inclined to suspect the identity of *T. nux* with *D. robusta*, but in the absence of type material, which I have been unable to obtain, the question remains unsettled.

Columnitis squamata Schmidt, 1870 A (*vide* Topsent, 1918).

Donatia parasitica Higgin, 1877 A.

From a preparation in the Carter cabinet in the possession of Prof. A. Dendy I find this species to be obviously a *Timea* (*vide* Pl. I. fig. 1).

Key to the known Species of Donatia.

A. Micrasters with typically oxeote rays, with tendency to
    become strongylote or rarely tylote ... ...   *D. peracuata.*

B. Micrasters with typically strongylote rays.
    1. Micrasters with short rays.
        a. Rays have tendency to become tylote, rarely oxeote,
          and roughened or spined.
            i. With small spherasters ... ...   *D. lyncurium.*
            ii. With large spherasters . .. .   *D. repens.*
        b. Rays may become tylote, but never roughened or
          spined : never hexaradiate .. ..   *D. deformis.*
    2. Micrasters of two kinds, viz. short-rayed and long-rayed.
        a. Surface tessellated, cortex densely charged with
          spherasters, loose megascleres between the bundles .   *D. robusta.*
        b. Surface conulose, pores in cribriform groups, spher-
          asters scattered sparingly in the cortex, no loose
          megascleres between the radial bundles   ... .   *D. magna.*
        c. Spherasters differentiated into cortical and choano-
          somal; sponge stipitate   ....   *D. fissurata.*

C. Micrasters with typically tylote rays.
    1. Rays spined; may rarely become oxeote . ...   *D. multistella.*
    2. Rays usually smooth, hexaradiate, never oxeote . ...   *D. japonica.*

D. Micrasters of two kinds, tylasters with short rays and
    oxyasters with elongated and roughened or tuberculate
    rays.
    1. Microscleres regular, rays of oxyasters frequently
        branched   . ...   *D. diploderma.*
    2. Spherasters variable, rays of micrasters reduced, but not
        to point of disappearance .. ..   *D. maza.*
    3. All microscleres tend to have reduced rays, with for-
        mation of smooth spheres . .   ..   *D. montrosa.*

Genus 2. XENOSPONGIA Gray, 1858.

Diagnosis:—Donatiidæ of discoidal form. Choanosome con-
taining sand in its deeper parts. Inhalant pores localized in
well-defined grooves, partly concentric and partly radial in
arrangement. Vents on slight prominences. Surface tuber-
culate. Skeleton composed of bundles of styli ending in brushes,
which project from the surface tubercles and also form a slight
marginal fringe. Microscleres euasters of various forms and sizes,
forming a dense cortical layer, and also abundantly scattered in
the choanosome.

(For description and illustrations *vide* Dendy, 1905 A.
The only known species is:—

XENOSPONGIA PATELLIFORMIS Gray, 1858.

Synonymy:—*X. patelliformis* Carter, 1882 A.
                X. patelliformis Sollas, 1888 B.
                X. patelliformis Dendy, 1905 A.
Distribution:—Torres Straits; Ceylon.

Genus 3. TETHYORRHAPHIS Lendenfeld (1884 A).

Diagnosis:—Donatiidæ possessing microrhabds, in addition to
the usual Donatiid spicules.

(For description and discussion *vide* Hallmann, 1914 A.)
The only known species is:—

TETHYORRHAPHIS LÆVIS Lendenfeld, 1888 A.

Synonymy :—*T. gigantea* Lendenfeld, 1888 A.
    T. conulosa Lendenfeld, 1888 A.
    T. tuberculata Lendenfeld, 1888 A.

Distribution :— Port Jackson, Australia.

Genus 4. HALICOMETES Topsent, 1920.

Synonymy :—*Cometella* Schmidt, 1870 A.
    Tethya Schmidt, 1880.

Diagnosis :—Stipitate Donatiidæ, possessing vestigial triænes in addition to the characteristic Donatiid spicules.

(For description and illustrations *vide* Topsent, 1920 c.)

Discussion :—The genus is probably an aberrant member of the family Donatiidæ. The only known species is :—

HALICOMETES STELLATA (Schmidt).

Synonymy :—*Cometella stellata* Schmidt, 1870 A.
    Tethya cometes Schmidt, 1880.
    Tethya ? stellata Sollas, 1888 B.

Distribution :—W. Indies.

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EXPLANATION OF THE PLATE.

Fig. 1.   *Donatia parasitica* (Higgin).
   1*a*. Megasters, ✕ ; 1*b*. Micrasters.
Fig. 2.   *Donatia fissurata* (Lendenfeld).
   2*a*. Cortical megaster; 2*b*. Choanosomal megaster, 2*c*. Long-rayed micraster; 2*d*. Short-rayed micraster.
Fig. 3.   *Donatia maza* (Selenka).
   3*a*. Megasters; 3*b*. Tylasters; 3*c*. Long-rayed oxyasters, 3*d*. Reduced strongyloxea.   .
Fig. 4.   *Donatia monstrosa*, sp. n.
   4*a*. Megasters, showing stages in reduction to spheres, 4*b*. Long-rayed micrasters, showing stages in reduction to spheres; 4*c*. Short-rayed micrasters, with reduction to spheres.

44. On the Anatomy of *Parallepipedum* Klein (Mollusca). By EKENDRA NATH GHOSH, M.Sc., M.D., F.Z.S., F.R.M.S., Professor of Biology, Medical College, Calcutta, and Post-graduate Lecturer on Invertebrate Zoology, Science College of the Calcutta University.

(Text-figures 1–5.)

The lamellibranchiate subgenus *Parallepipedum* Klein ('Methodi Ostracologicæ,' 1753, p. 122) of *Arca* Linné belongs to the Family Arcidæ Gray, Order Filibranchia of Pelseneer (Mollusca in 'Treatise on Zoology,' edited by E. R. Lankester, p. 258). It formed a genus in Gray's classification of his Tribe Arcaina (Family Arcidæ) (Ann. Mag. N. H. ser. 2, vol. xix. 1857, p. 368) under the name *Trisis* Oken. Adams and Adams (' Genera of Mollusca,' 1858, vol. ii. p. 538) followed Gray's classification and made it a genus under the name *Parallelepipedum* Klein. Fischer (Man. de Conchyliol. 1887, p. 977) and Kobelt (in Martini-Chemnitz, Syst. Conch.-Cab. viii. Abth. 2, *Arca*, 1891, p. 4) made it a subgenus of *Arca*. Dall (Trans. Wagner Free Instit. of Science, iii. pt. 3, 1895, p. 516) made it the eighth group of his second subgenus *Barbatia*. Lamy (Journ. de Conchyliol. vol. lv. 1907, p. 3) made it a subgenus of *Arca* Linné. He places it between *Fossularca* Cossmann and *Scaphula* Benson. Pelseneer raised some of the subgenera of Fischer and Dall to the rank of genera, as *Barbatia* Gray and *Scaphula* Benson. Comparing the anatomical peculiarities of the animal of *Parallepipedum* Klein with those of the just-mentioned genera, the present subgenus may be raised to the rank of a genus.

Parallepipedum Klein includes a single species, *P. tortuosum* (Linné) (*Arca tortuosa* in 10th edition of the 'Systema Naturæ,' p. 693), which was described only from the shell. The peculiar twisting of the body with a corresponding change in the shell evidently affects the organization of the animal. The present paper aims at describing the soft parts of the animal, three specimens of which were received from the Biological Station at Tuticorin (now at Ennor), Madras, by purchase.

The body of the animal is elongated and asymmetrical. The anterior third of the body is twisted towards the right side through about one-third of a right angle, and the posterior third is so twisted towards the left side that the posterior margin is deflected about one-half of a right angle from the median vertical line. The dorsal lozenge-shaped area between the depressed umbonal regions has nearly disappeared owing to the approximation of the latter. The median dorsal margin is slightly less

than the body in length. The mantle lobes are twisted in the
same manner as the body of the animal. The anterior adductor
muscle is more or less oval in shape and is much smaller than the
posterior adductor. Owing to the twisting of the body towards
the right in front, the attachment surfaces of the anterior
adductor muscle vary on the two sides; the face of the left is
directed downwards and that of the right side is directed up-

Text-figure 1.
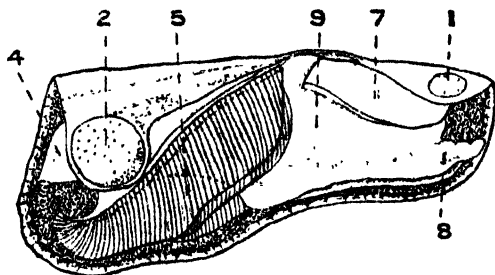
Animal of *Parallepipedum tortuosum*, side view (right), with the
right mantle-lobe removed. × 1.

Text-figure 2.
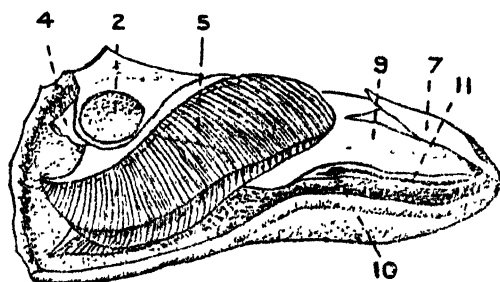
Animal of *P. tortuosum*, ventral view. × 1.

1. Anterior adductor muscle. 2. Posterior adductor muscle. 3. Posterior retractor
pedis muscle. 4. Free end of the rectum. 5. Outer demibranch, 6. Liver.
7. Labial palps. 8. Foot. 9. Visceral mass 10. Byssus cavity. 11. Ven-
tral fissure of the foot. 12. Ventricle. 13. Auricle (left). 14. Rectum.
15. Ciliary disc. 16. Anterior aorta. 17. Posterior aorta.

wards. The posterior adductor muscle is large with the two
faces unequal in shape and size; the left attachment surface is
triangular in shape, smaller than the right one, and is slightly
directed upwards; the right one is large, oval in shape, and is
directed slightly downwards. The foot is elongated, compressed
laterally, about half the body in length, and is about one-sixth

deep. A round process is present at the postero-inferior angle of the foot. The foot is bent to the right in the anterior two-thirds of its length, and to the left in the posterior one-third. A deep median ventral fissure is present on the foot. A rudimentary byssus cavity and byssus are present at the posterior end. The posterior retractor pedis muscle is very long, wide, and sloping; it occupies a good portion of the visceral mass posteriorly and ends above the byssus cavity. The body-twist has strongly displayed its effects on the posterior retractor pedis muscle, causing a great disparity in size and shape of the two heads of insertion into the valves; the left head is large, wide, and triangular, while the right head is very narrow and elongated owing to the flattening out of the body on that side.

Text-figure 3.
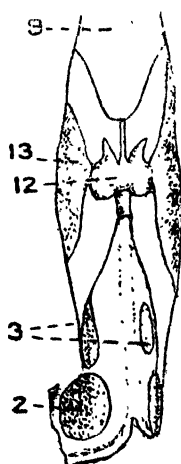
Dorsal view of the animal, showing the pericardial sacs, heart, posterior retractor pedis and posterior adductor muscles. × 2.

The visceral mass is slightly swollen on the right side, but is flattened out on the left. The gills are elongated and placed somewhat diagonally, being more than half the body in length, and about twice as long as deep. The gills of both the sides are bent to the right in front and to the left behind. The inner demibranch is wider than the outer. Both the gills are separated from the labial palps by a distinct interval. The gill-axis is narrow, elongated, rod-like, and twisted; it is placed more horizontally than diagonally and is provided with a free flexible posterior portion extending behind the posterior adductor muscle. The gill-filaments are placed nearly at right angles to the gill-axis. The reflected filaments are slightly longer than the direct ones. The labial palps are elongated, widened behind, and are

tapering in front; they are one-third the body in length, less than thrice as long as broad, and are placed at an obtuse angle with the gill-axis. The œsophagus is somewhat elongated and curved with the convexity directed upwards and forwards. The stomach is irregularly oval. The small triangular cæcum of the crystalline style communicates freely with the beginning of the first limb of the intestine. The intestine has the first limb

Text-figure 4.
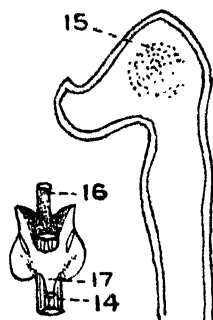
Free end of a filament of the inner demibranch (highly magnified)

Text-figure 5.
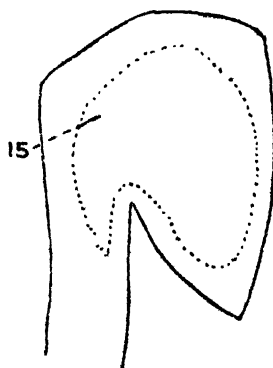
Free end of a filament of the outer demibranch (highly magnified).

crossed by the second. The digestive gland forms a small mass round the ventral and lateral aspects of the stomach. The rectum ends in the anus at the postero-ventral aspect of the posterior adductor muscle. The long terminal portion of the rectum is directed downwards and slightly backwards and is bent towards the left side; it is connected with the posterior adductor muscle by a thin membrane. The pericardium consists of two

unequal sacs, with a median aperture of communication above the heart. The right sac of the pericardium is larger than the left and extends beyond the right head of the posterior retractor pedis muscle to the anterior border of the posterior adductor muscle. The left sac ends in front of the left head of the posterior retractor pedis muscle. The ventricle is constricted in the middle. The rectum passes *through* the ventricle very near the lower surface, having a short wide bridge underneath. The auricles are large and greatly elongated posteriorly; they are placed asymmetrically and do not communicate with each other; the right auricle is longer than the left. The anterior aorta arises from the bridge underneath the rectum. The osphradia, Thiele's abdominal sense organs, and compound pallial eyes are all absent. The genital organs are extensive.

Structure of the gills.—The gill-filaments are flattened antero-posteriorly as usual. The free ends of the reflected filaments of the outer demibranch are beak-shaped and bent outwards, and those of the inner demibranch are bent inwards and triangular in shape. The inter-lamellar extensions at the bases are narrow above, wide in the middle, and tapering below. They are about one-eighth the length of the direct filaments in both the demi-branchs. An inter-lamellar septum is present at the flexure of the filament. The ciliary discs are arranged in irregular trans-verse rows, about fourteen in number.

Notes on the living animal.—The following notes on the animal have been kindly supplied by the Director, Biological Station, Ennor (Madras):—The species is fairly numerous in certain parts of Palk Bay between $4\frac{1}{2}$ and 6 fathom lines on a bottom of dirty muddy sand, and is not found in crevices. It occurs scattered singly over large areas, and does not form con-tinuous beds. Its shells often give foothold to pearl oysters on the banks north-east of Tondi.

Remarks.—Leaving aside the peculiarities in the organization due to the body twist, we find that the animal agrees with the animals of *Byssarca, Barbatia,* and *Scaphula* in the antero-posterior elongation of the body and in the marked difference in the size of the adductor muscle, and that it differs from them in the greatly constricted dorsal area between the umbones. The dorsal area is widest in *Byssarca,* less so in *Acar* and *Scaphula,* narrow in *Barbatia* and *Fossularca,* and is narrowest in *Parallepipedum.* The present animal resembles the animal of *Acar* in lateral flattening of the body. The extremely narrow dorsal area and the flattening of the body probably represent the original ancestral character still retained in the present animal. Considering the antero-posterior elongation of the body, we see that it is entirely confined to the visceral mass; in the anterior region it is indicated by the elongation of the foot, the position (more horizontal than diagonal) and elongation of the labial palps and their separation from the gills, and by the course of the œsophagus; in the posterior region the posterior retractor pedis

muscle and the intestine are affected in the process. In this characteristic the present animal comes nearest to the animal of *Scaphula*, in which, however, the posterior region of the visceral mass is more elongated than the anterior.   In *Byssarca* and *Barbatia* the posterior region of the visceral mass is much elongated, but the foot and the anterior region of the visceral mass are short.   In *Acar* the elongation has affected the posterior portion of the visceral mass and the posterior portions of the mantle-lobes, which are remarkably extended downwards and backwards.   Coming to the heart, we find the ventricle simply constricted in the middle in the present animal, a condition also found in *Anadara* and representing an earlier condition ; in *Arca* the median constriction is transformed into a narrow median portion separating two lateral lobes ; this process of separation is carried further in *Barbatia* until we arrive at a condition with two ventricles in *Byssarca*.   In *Parallepipedum* the auricles are much more elongated than those in the above-mentioned animals, and this peculiarity is no doubt correlated with a much less antero-posterior widening of the heads of the posterior retractor pedis muscle in the present animal than in the others.   The rudimentary condition of the byssus and absence of the pallial sense-organs are probably examples of degeneration.

Considering the organization of the present animal as compared with those of the genera of the Arcidæ, we may assume that the present asymmetrical conditions of the body might have been derived from a bilaterally symmetrical condition in the original ancestral form.   It is difficult to speculate upon the circumstances under which such a twist occurred in the body of the present animal, which is known to live in the open sea.

In a flattened wedge-shaped body, the twist of the same nature as in the present animal can be easily brought about by a rotating movement along the axis of the hinge line, the posterior region held fast in some way, and the anterior region bent towards the opposite direction.   Such a possibility is applicable in a form trying to adapt itself to a crevice, generation after generation for a long time, geologically considered.   Again, the present species, now living in the open sea, might have descended from an ancestor which originally adapted itself to a crevice, but the change of life in the present form might have been due to some geological disturbances in its original abode.

In conclusion, it may be suggested that the original bilaterally symmetrical ancestor of *Parallepipedum* might have arisen in common with those of *Byssarca*, *Barbatia*, *Arca*, and *Scaphula*, and then gave rise to the present asymmetrical form.

A.

B.

C.

D.
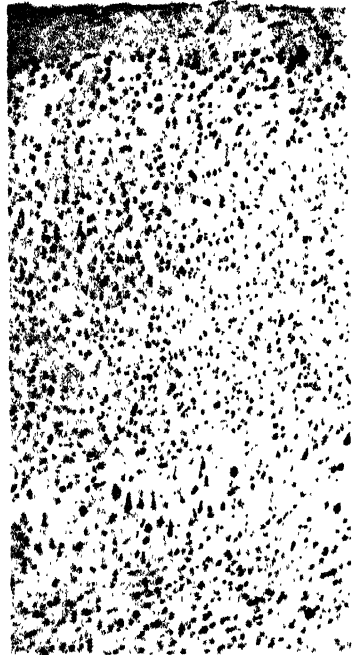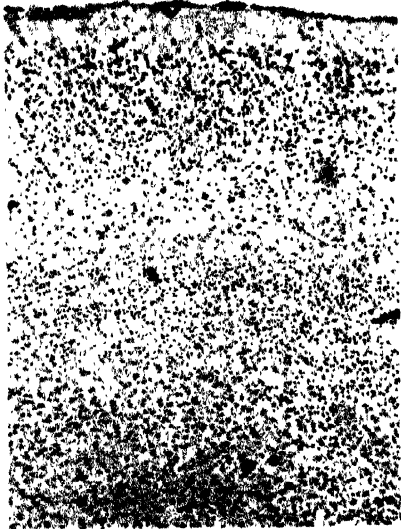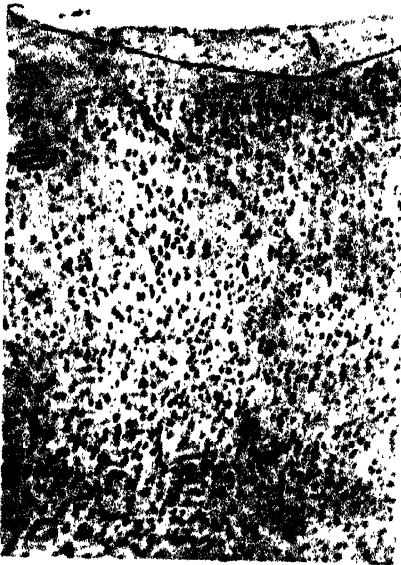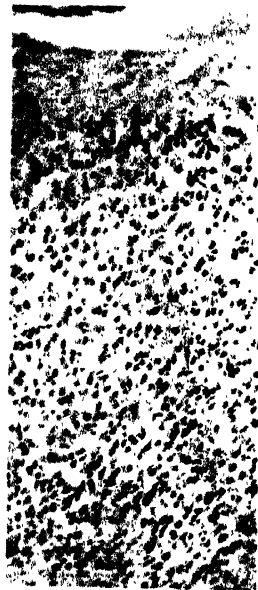
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BRAIN OF THE TREE-SHREW TUPAIA MINOR

BRAIN OF THE TREE-SHREW TUPAIA MINOR.

A

B.

C

BRAIN OF THE TREE-SHREW TUPAIA MINOR.

45. On the Brain of the Tree-Shrew (*Tupaia minor*).
By W. E. Le Gros Clark, F.R.C.S.Eng., F.Z.S.

(Plates I.–III.*; Text-figures 1–14.)

The peculiar structural features of the Menotyphla have led systematists to regard this group of mammals as of very particular interest, and it is therefore somewhat surprising that so little note has hitherto been taken of their cerebral morphology. Elliot Smith (5) has described the brain of *Macroscelides*, a terrestrial animal, and has laid emphasis on the curious combination of primate and metatheroid characters which it presents. The general conformation of the brain of *Tupaia* has been figured and described, without any detail, by Garrod (9) and Carlsson (2). *Tupaia minor* is one of the smaller species of the Tupaiidæ, differing from the larger species in being more thoroughly arboreal in its habits, in possessing a relatively longer tail, and a less elongated snout. In general appearance the animal possesses a less specialized (*i. e.*, a more primitive) form than do many other members of the Tupaiidæ.

The specimens upon which I have worked, I collected myself in Borneo some two years ago. The animals have been preserved in formalin, which in some cases was injected intravascularly soon after death.

In general form, the brain of *Tupaia minor* appears relatively simple, consisting of small pyriform cerebral hemispheres, macroscopically entire except for the ectorhinal fissure and an indication of the sulcus calcarinus, and a cerebellum of a primitive type.

By the comparatively small proportions of the olfactory regions of the brain, however, it shows a marked superiority over the brains of *Macroscelides* and lipotyphlous Insectivora. The average weight of three complete brains of adult animals was found to be 1·77 grams, and the average weight of the bodies of these particular specimens was 46·4 grams. The brain-weight is thus about $\frac{1}{26}$th of the body-weight. It must be noted, however, that these measurements were made with specimens that had been preserved in 4 per cent. formalin for over a year.

The brain is illustrated from different aspects in text-figs. 1–5 and by a photograph (Pl. III. *b*) of an endocranial cast made with plaster of Paris. This latter is useful for illustrating the proportions of the brain, especially with regard to the olfactory bulb, which, owing to its soft and friable structure, is difficult to preserve whole when removing the actual brain.

THE CEREBRUM.

A lateral view shows the hemisphere to be somewhat elongated antero-posteriorly, narrowing down to the attenuated frontal lobes which partially cover the olfactory bulbs in front. Traced backwards, the upper margin, which is 15–17 mm. in length, shows a faint shallow depression about midway along the hemisphere, and reaches back to an occipital pole which slightly overlaps the cerebellum. The posterior margin, about 12·5 mm. long, slopes downwards and forwards to a well-marked temporal pole, the tip of which is formed by the pyriform lobe. The

Text-figure 1.
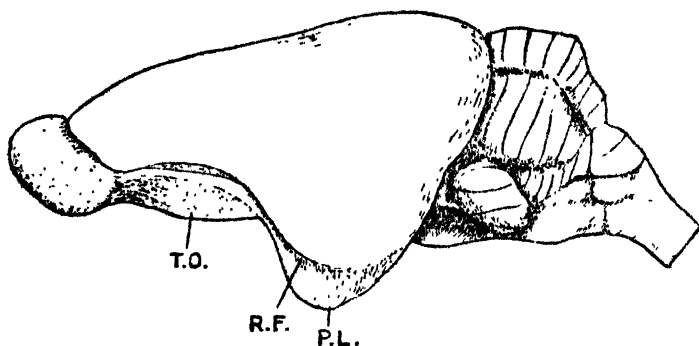
Brain of *Tupaia minor*. Lateral view.

A.C. Anterior commissure.	P. Pons.
A.C.Q. Anterior corpus quadrigeminum.	P.C.Q. Posterior corpus quadrigeminum.
C.T. Corpus trapezoideum.	Pf. Paraflocculus.
F. Fornix.	P.L. Pyriform lobe.
Fi. Fimbria.	Py. Pyramidal tract.
G.D. Gyrus dentatus.	R.F. Ectorhinal fissure.
H.T. Hippocampal tubercle.	S.C. Sulcus calcarinus.
I.H. Inverted hippocampus.	T.C. Tuber cinereum.
L.O.S. Lateral olfactory stria.	T.O. Tuberculum olfactorium.
O.B. Olfactory bulb.	V. Trigeminal nerve.
O.C. Optic chiasma.	

posterior margin is indented at the middle of its course by the protruding paraflocculus. The pyriform lobe, bounded laterally by the ectorhinal fissure, which becomes more indistinct as traced posteriorly, encroaches relatively to a very small extent on the lateral surface of the cerebral hemisphere, the greater part being confined to the basal aspect.

The olfactory bulbs, compared with those of other small insectivorous mammals, are small. They are about 4·5 mm. long and 3 mm. broad, projecting beyond the anterior pole of the hemisphere by about 2·5 mm.

The tuberculum olfactorium, as seen from the lateral aspect, is only slightly raised above the surface, in marked contrast to the prominent rounded tubercle usually found in small macrosmatic mammals of a comparable size.

The lower border of the hemisphere, traced posteriorly, shows an even curve backwards and a little upwards, and then backwards and downwards, forming thus a hollow which accommodates the roof of the bony orbit. This curve is reflected in the ectorhinal fissure and, to a greater extent, in the lateral olfactory stria,

Text-figure 2.
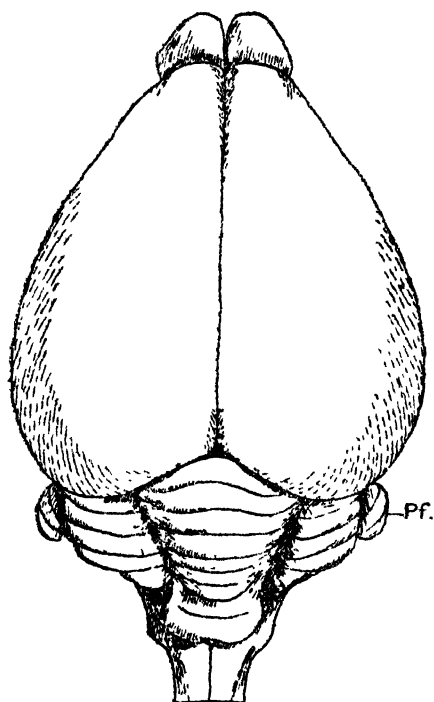
Brain of *Tupaia minor*   Dorsal view.
(References as in text-fig. 1.)

which is kinked sharply medialwards immediately in front of the temporal pole.

Viewed from above, the hemispheres are seen to be evenly curved and well rounded. Posteriorly the cerebrum comes into contact with the cerebellum, leaving no gap in which the pineal body or corpora quadrigemina are exposed, as is the case in *Macroscelides* and *Centetes*.

The basal aspect shows anteriorly the olfactory bulbs, which

Text-figure 3.
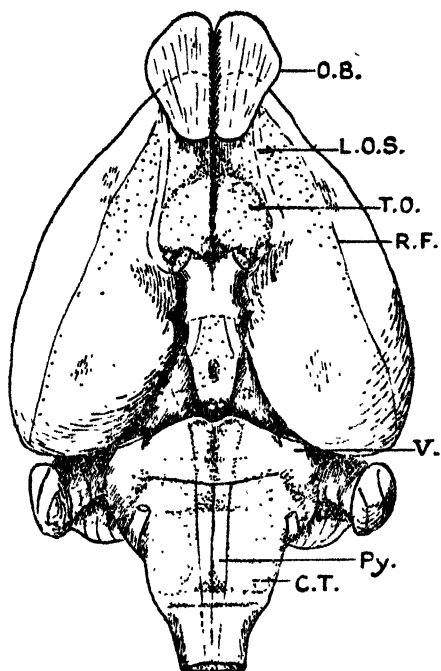
Brain of *Tupaia minor*. Basal view.
(References as in text-fig. 1.)

Text-figure 4.
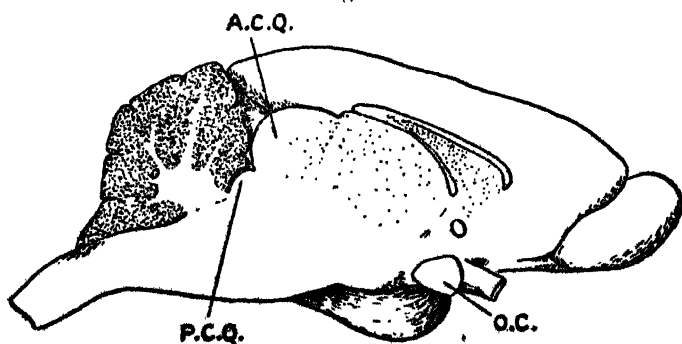
Brain of *Tupaia minor*. Mesial surface (sagittal section).
(References as in text-fig. 1.)

are almost sessile, being attached to the base of the brain by very short and thick peduncles. Immediately behind, on each side, is the flattened oval area which represents the tuberculum olfactorium, the long axis of which slopes backwards and outwards. The dimensions of this tubercle are 4·0 mm. by 2·75 mm. Bounding this area on the outer side is a well-marked white olfactory stria which terminates in the lobus pyriformis. The latter commences anteriorly at the lateral side of the lateral olfactory stria, and, where the latter takes a sudden turn medialwards, the pyriform lobe broadens out by extending also medialwards, a shallow depression being thus formed on its medial aspect which corresponds to the vallecula Sylvii. In the vallecula is a faint elevation which marks the posterior extremity of the lateral olfactory stria and is the tubercle of the olfactory tract.

Text-figure 5.
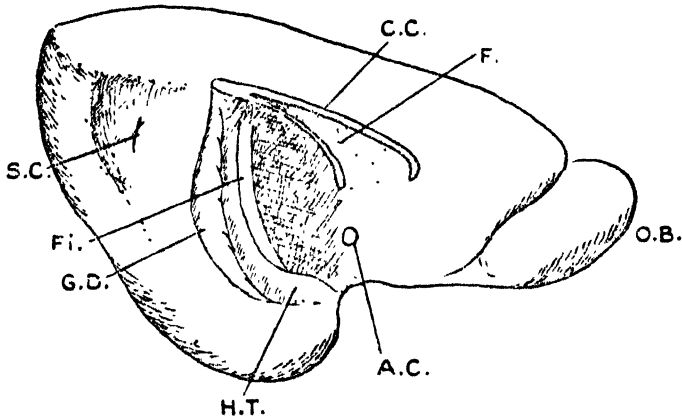
Brain of *Tupaia minor*. Mesial surface (brain stem removed).
(References as in text-fig. 1.)

The pyriform lobe is separated from the neopallial cortex by the ectorhinal fissure. It is important to note the extent to which this cortex is seen from the basal aspect, so that the ectorhinal fissure is visible in practically the whole of its length from this point of view.

The mesial part of the olfactory tract extends on to the mesial surface of the cerebrum opposite the olfactory tubercle.

The optic nerves are conspicuous for their large size, forming a chiasma from which the optic tracts can readily be traced back to the posterior part of the optic thalami and the anterior corpora quadrigemina.

Immediately behind the optic decussation is the well-marked

tuber cinereum, and more posteriorly the small corpora mammillaria. The oculo-motor nerves can be seen emerging from the interpeduncular space.

On its mesial aspect, the hemisphere shows a long attenuated corpus callosum terminating anteriorly in a well-marked, slightly recurved, genu. Posteriorly there is a faint thickening which represents the splenium. The length of the corpus callosum compared with the length of the cerebral hemispheres from frontal to occipital poles in two specimens is as follows :—

Corpus callosum.	Hemisphere.
7·0 mm.	17 mm.
6·75 mm.	15 mm.

Text-figure 6
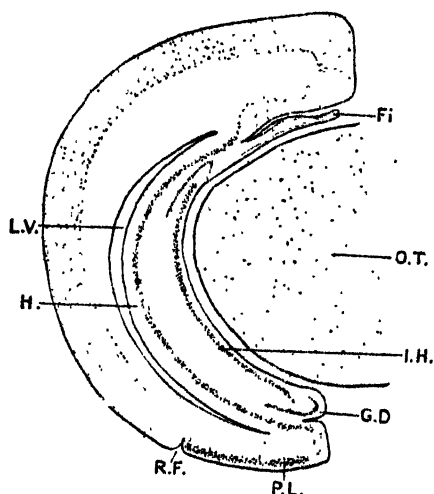
Transverse section of brain through the length of the hippocampal formation. (Semi-diagrammatic drawing.)

H. Hippocampus.   O.T. Optic thalamus.
L.V. Lateral ventricle.

(Other references as in text-fig. 1.)

Below is the psalterium ending anteriorly in a slight bulbous swelling, differing thus from the crescentic psalterium found in *Macroscelides* and *Metatheria*. More inferiorly are seen the small anterior commissure and the conspicuous optic chiasma. Posteriorly the occipital lobe is strongly indented by an impression for the large anterior corpus quadrigeminum, the bottom of which is slightly furrowed by a small sulcus calcarinus.

Bounding the margin of the choroidal fissure in the descending horn of the lateral ventricle is a well-defined white band (the fimbria), and behind this is a relatively broad band of cortex,

the microscopical structure of which shows it to be an area of inverted hippocampus.   This is well shown in text-fig. 6, which illustrates a transverse section of the brain through the length of this formation.   It extends from the amygdaloid nucleus at the tip of the temporal pole as far as the subsplenial region.   The inverted hippocampus expands at the temporal pole to form a very definite hippocampal tubercle, such as is found in primates and in primitive brains such as those of *Orycteropus* and *Macroscelides*.

Lying posterior to the band of inverted hippocampus is the crenate dentate gyrus, which becomes more attenuated and indistinct as it is traced downwards and forwards.   The dentate gyrus is bounded behind by the so called hippocampal " fissure." Above, the hippocampal formation turns on to the upper surface of the corpus callosum without kinking to form a definite subsplenial flexure.   Cells characteristic of the hippocampus can be traced as far forwards as the genu on the upper surface of the corpus callosum.

SULCI.

As I have stated above, the surface of the neopallial cortex is macroscopically smooth except for an indication of the calcarine sulcus.   Microscopical examination shows, however, the existence of some very definite cortical foldings.   These sulci do not necessarily involve the surface of the brain to any extent, beyond

Text figure 7.
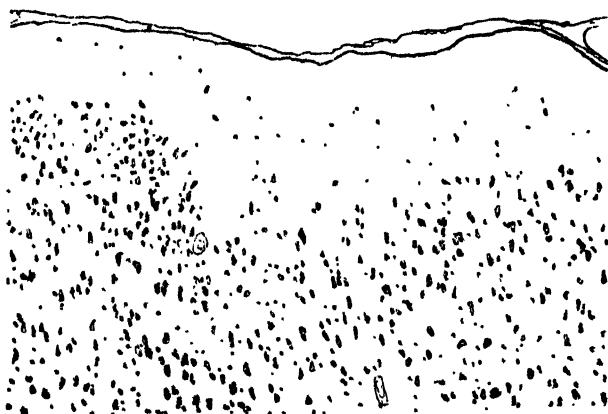
Section through suprasylvian sulcus.   (Traced by means of a projectoscope.)

a slight indentation caused by the presence of a blood-vessel, nor do they in all cases affect the whole thickness of the cortex. The foldings are best marked at the junction of the zonal with the underlying cellular layers, and thus might be termed

subzonal sulci. That these represent, without doubt, true cerebral sulci such as are seen macroscopically in fissured brains, but in an incipient condition, can best be shown by describing them. A study of the transverse serial sections, Nos. 446–536, shows a subzonal sulcus which runs backwards and slightly downwards about three-fifths of the way from the upper to the lower margins of the lateral surface of the hemisphere in this region. This sulcus can be traced perfectly distinctly for a short distance,

Text figure 8.
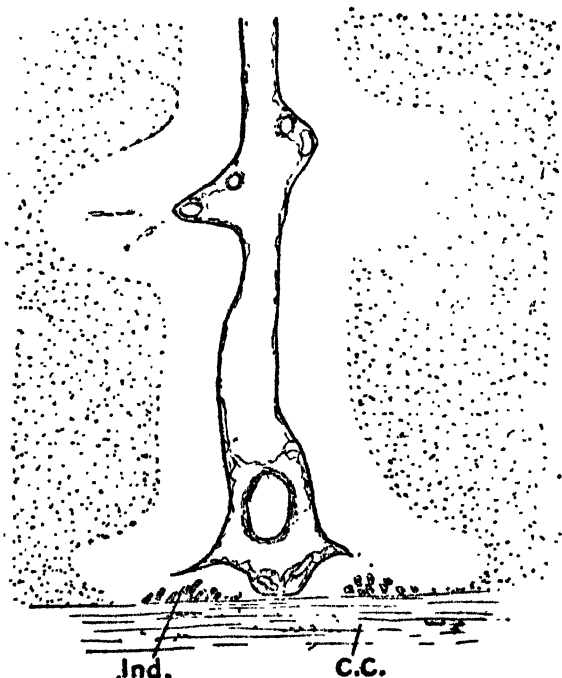
Transverse section through fore part of corpus callosum, illustrating the intercalary sulcus. (Semi-diagrammatic.)

C.C. Corpus callosum. | Ind. Indusium.

fading away indefinitely in front and behind. The appearance of this sulcus in section is accurately shown in text-fig. 7, which is a tracing made from an actual section by means of a projectoscope. It will be seen that there is a very slight surface depression, a marked dip of the zonal layer, and no invagination of the pial membrane.

At first sight, such a formation would hardly seem to correspond in any way to a true cerebral sulcus. The following

considerations, however, show that they are identical. The line of folding is straight and continuous, section by section. In sections of the head of a Tree-Shrew of a larger species (? *T. ferruginea*), for the loan of which I have to thank Dr. Woollard, I have found a sulcus in a precisely similar position and of the same relative length, involving also the surface of the cortex and containing an invagination of the pia mater *. At either end where the sulcus fades away in this larger specimen, it presents an appearance comparable to that found in the entire length of the sulcus in *Tupaia minor*.

An examination of the cortical structure shows that this sulcus lies at the junction of the general sensory area and a granular area corresponding evidently to Brodmann's area, Nos. 13–16.

Text-figure 9.
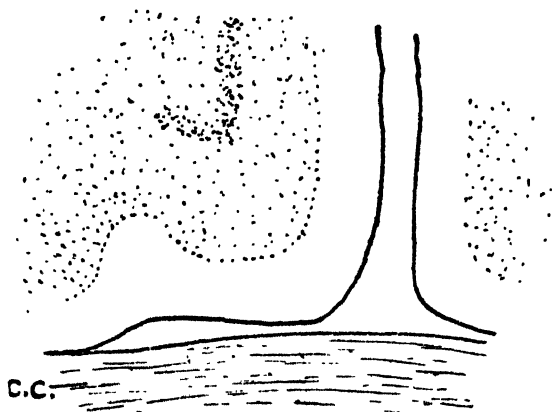
Section through posterior part of intercalary sulcus. (Diagrammatic.)

C.C. Corpus callosum.

The position of this subzonal sulcus, especially with regard to the subjacent cortical areas, leaves no doubt that it represents a small suprasylvian sulcus.

I was interested to find that in the endocranial cast (figured in Pl. IV. *b*) a depression is shown corresponding in position and direction to the sulcus described above.

In Nos. 326–448 of the transverse section series can be seen a well-marked sulcus which runs forwards and upwards on the mesial surface of the cerebrum between the corpus callosum and the upper margin of the hemisphere, as shown in text-fig. 11. This sulcus limits the calloso-marginal area of cortex, and appears to correspond to the anterior part of the intercalary sulcus. The appearance of this sulcus as seen in section is shown in

* Even in the brains of *Tupaia ferruginea* which I have, there are no signs macroscopically of neopallial sulci except the s. calcarinus.

text-fig. 4, and, as with the previous sulcus, the folding involves the cortex mainly at the junction of the zonal and outer granular layers. There is a slight groove in a corresponding position on the surface of the brain which lodges a small vessel, and in some sections small vessels can be seen passing down into the middle of the sulcus carrying with them strands of pia mater.

At the posterior end of the corpus callosum, sections show another small sulcus which limits the striate area in this region. As shown in text-fig. 9, this sulcus lies on the upper surface of the corpus callosum, for, owing to the extent of the striate area, the cortex has here been inrolled between the mesial surface of the brain and the corpus callosum to a distance of 2 mm., and the junction between the striate and calloso-marginal area thus completely buried. This sulcus clearly corresponds to the posterior part of the intercalary group of sulci.

There can be no doubt that these foldings represent true sulci, and it may be noted that other but less distinct local thickenings of the zonal layer occur and, very frequently, along the line of junction of one cortical area with another.

It may be noted that in a recent publication Fortuyn (8) has drawn attention to local variations in the thickness of the lamina zonalis dependent upon changes of a chemical or physical nature which take place in the subjacent cortical cells. It is quite certain that the subzonal sulci here described bear no relation to these phenomena.

THE STRUCTURE OF THE CEREBRAL CORTEX.

The cortical structure has been studied by means of a complete series of transverse sections and a partially complete series of sagittal sections through the entire brain of *Tupaia minor*. The sections were cut at a thickness of $10\,\mu$, and were stained with thionin. In addition, I have had an opportunity of examining a series of transverse sections through the head of a larger species of Tree-Shrew, stained with carmine, for the loan of which I have to thank Dr. Woollard of University College.

An intensive study of these sections has enabled me to differentiate several structurally distinct areas of the cortex and to map out their surface extent on the cerebral hemisphere with a tolerable degree of accuracy.

A survey of various works dealing with the comparative lamination of the cerebral cortex—(1), (7), (12), (14)—shows a certain amount of disagreement in the results of investigations by different observers, and it is evident that the division of the cerebral cortex into a large number of small areas characterized by minute differences in cortical structure involves a personal equation sufficiently large to render the result very questionable. In the present work no attempt has been made to delineate other than broad and easily recognisable areas. The two areas which

it is, perhaps, most important to map out on the surface of the hemisphere are the visual area and the motor area, and by good fortune these areas are characterized by a cortical structure which is most distinctive.

The extent of the visual cortex gives some indication of the part which vision plays in the life of the animal, and the anterior boundary of the Betz cell area also marks out the posterior limit of the frontal area, the development of which appears to be some indication of intellectual status.

The cellular content of the cortex in *Tupaia* is comparatively rich, though rather less so than in the case of *Tarsius* and *Nycticebus*, as can readily be seen by comparing sections of similar thickness. The individual cells are well differentiated to form the various recognised types, and the lamination of the

Text-figure 10.
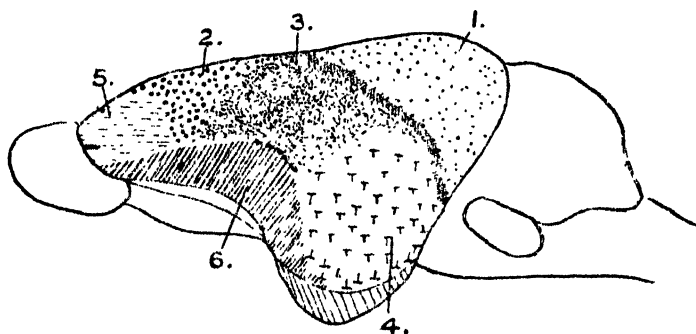
The cortical areas on the lateral surface of the cerebral hemispheres
(For references, see text.)

cortex into definite layers is usually distinct. The pyramidal layer is relatively deep and is, in most regions, separated from the ganglionic and multiform layers by a conspicuous internal granular layer.

The external granular layer of Brodmann is not well developed, though recognisable. The cortical areas of the neopallium which can be distinguished and delineated by a distinctive cellular architecture are eight in number, as follows : —

1. Striate area.
2. Betz cell area.
3. Parietal area.
4. Temporal area.
5. Frontal area.
6. Insular area.
7. Retrosplenial area.
8. Calloso-marginal area.

It must be emphasized that the measurements given in the following notes on the different cortical areas are of an approximate nature only. The depth of the cortex in one area varies to a certain extent according to the position which it occupies—whether on a flat, a convex, or a depressed surface,—and in many cases the cortical layers are not sharply differentiated

Text-figure 11.
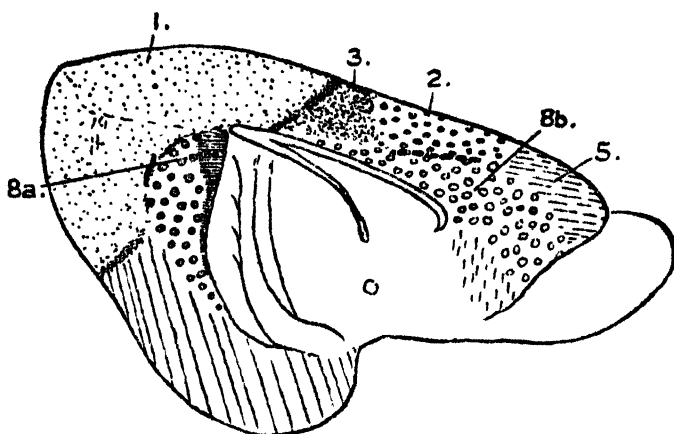
The cortical areas on the mesial surface of the brain.

from one another, so that it is not easy to distinguish their boundaries accurately. The measurements given are the averages of a large number of measurements made by means of a projectoscope, the magnification given by the latter having been standardized by comparison with a scale of known magnitude.

1. *Striate area.* (Pl. I. *a* & *b*.)

The cortex in this area corresponds in its cell lamination to area 17 of Brodmann. It is characterized by the presence of a layer with comparatively few cells, and in sections stained with thionin this is easily recognisable with the naked eye as a pale stria, which ceases abruptly at the margin of the area. Microscopically, it shows a relatively thin superficial fibre layer (the zonal layer), and a very conspicuous and sharply-defined inner granular layer. The depth of the cortex in this area averages 1·29 mm., and the average thickness of each of the several layers is as follows:—

I. Lamina zonalis	·09
II. & III. Lam. granularis externa and pyramidalis	·69
IV. Lam. granularis interna	·26
V. Lam. ganglionaris..............	·17
VI. Lam. multiforme	·09

In attempting to correlate this cortical area with one of the three forms of the calcarine type described by Brodmann (1), some difficulty has been found in determining precisely the extent of the internal granular layer proper. As can be readily seen from the illustrations (Pl. 1. *a* & *b*) the layer appears to be definite enough, and since in most regions it is separated by an irregular cleft into superficial and deep strata, it was thought that these corresponded to the two divisions of the inner granular layer seen so clearly in primates. If this were the case, the stria of Gennari is represented here by the irregular cleft above mentioned, and the conspicuous white band which can be seen macroscopically lies wholly external, and, although it marks out accurately the limits of this cortical area, is not (so far as its relative position among the cortical layers is concerned) strictly homologous with Gennari's line.

An alternative interpretation is suggested by a comparison with Brodmann's figures of the calcarine type of cortex in various mammals. This is, that the cortex of the Tree-Shrew belongs to the "tristriare form" of Brodmann—the conspicuous band of granule cells corresponding to the inner stratum of the divided inner granular layer, III. C, the comparatively sparsely cellular layer immediately external being the stria of Gennari (III. *b*), while the outer division of the granular layer is represented by the few granule cells scattered throughout the deeper strata of the pyramidal layer. If this construction of the facts is correct, the outer division of the granular layer is not clearly differentiated from the pyramidal layer, for cells of the pyramidal type are found freely intermingled with granule cells.

An examination of actual stained sections of the occipital cortex of *Tarsius* and *Nycticebus* (for the opportunity of studying which I should like to express my great indebtedness to Dr. Woollard) has convinced me, and, I feel sure, would likewise convince any observer, that the first interpretation of the lamination of the striate cortex in the Tree-Shrew is the correct one.

In *Tarsius*, as in *Tupaia*, the lamina granularis interna is bounded externally by a layer with comparatively few cells, and the similarity in appearance of this layer, the cells which it contains, and its relation to the superjacent pyramidal layer, leaves no doubt as to its identity in both these specimens. Moreover, the granular layer in *Tarsius* is conspicuously duplicated. The granular layer in *Tupaia* has been described above as being separated into outer and inner divisions by an irregular cleft. This cleft, poor in its cellular content, is remarkably definite in some areas of the occipital cortex, and its presence is marked by a very distinct local thickening of the granular layer affecting especially the superficial part of this layer. It is evident, I think, that in *Tupaia* there is an incipient duplication of the lamina granularis interna associated with the appearance of a "white line of Gennari."

It may be remarked here that it is possible to regard the cleft

between the two layers of granules and the layer comparatively
empty of cells external to the granular layer (i. e., the macroscopic
pale stria) as both homologous with the stria of Gennari of the
higher primate brain. This may be done if the superficial
granule cells are represented as being split away from the deeper
granules and commencing their (phylogenetic) journey across the
white line of Gennari to reach the deep margin of the pyramidal
layer on the opposite side so as eventually to leave the "white
line" between the outer and inner divisions of granules. On this
supposition, in *Tupaia* the superficial granules are beginning to
be separated from the deeper cells and drawn outwards towards
the lamina pyramidalis, perhaps by a process of neurobiotactic
attraction. I will not, however, enter here into the detailed
evidence for this point of view.

Text-figure 12.

A.   B.   C.
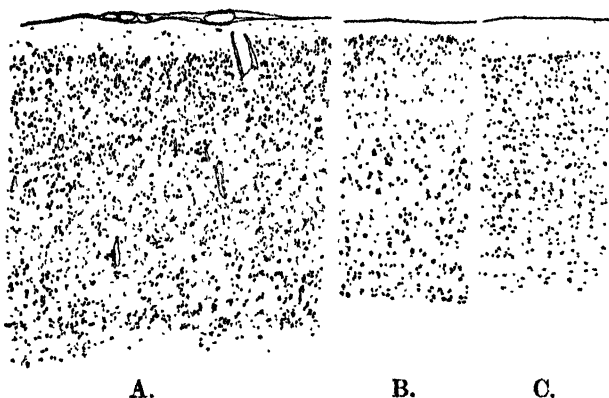
The occipital cortex of (a) *Tupaia minor* (at the junction of the striate and ? visuo-
    psychic areas); (b) *Sciurus prevosti*; (c) *Marmosa*. (From actual tracings made
    by means of a projectoscope.)

An attempt to map out a definite area in the occipital cortex
where the duplication of the granular layer is distinct was not
successful, for the cleavage of the layer is irregularly distributed
in patches throughout the striate area.

The marked degree of development of the pyramidal layer is
very striking, and, combined with an advanced degree of differ-
entiation of the inner granular layer and a relatively small depth
of the infragranular layers, it affords an interesting comparison
with the visuo-sensory cortex of lemurs. It is clear, therefore,
that the striate cortex of *Tupaia minor* is highly differentiated,
and this, I believe, is of importance in the consideration of the
morphological affinities of the animal. For purposes of comparison,
I give figures of the occipital cortex (taken from the occipital pole
of the brain) of *Sciurus* and *Marmosa*, both of which animals lead

an arboreal existence and show many striking resemblances in their habits and outward appearance to *Tupaia*. It is interesting to note that these two figures resemble very closely those given by Mott of the visual cortex of the rabbit and wallaby respectively. Fortuyn, in his work on the cortical lamination of rodents (7), unfortunately does not figure the visual cortex of *Sciurus*. His description, however, corresponds very well with the structure, as I found it, in my specimen.

The extent of the striate area can be mapped out without difficulty, for the cortical structure changes very abruptly at its margins. As shown in text-fig. 6, the area encroaches to a considerable degree on the lateral surface of the hemisphere. On the mesial surface it is limited anteriorly below by the sulcus calcarinus, but reaches above actually to the upper surface of the corpus callosum where it is inrolled to a slight extent, so that its boundary here is buried under the surface. This would seem to indicate a marked expansion of the visual cortex, and if the structural resemblances with the primates which *Tupaia* shows in many of its anatomical features indicate a real morphological affinity, this is remarkably consistent with Elliot Smith's interpretation of the factors which initiated or accompanied the evolutionary development of the primate brain.

2. *The Betz Cell Area.* (Pl. II. *b.*)

This cortical area is distinguished by the presence of giant pyramidal cells in the lamina ganglionaris. By these distinctive cells, the relative thinness of the zonal layer and small depth of the pyramidal layer, the limits of the area can be defined. The average total depth of the cortex in this area is 1·12 mm. The depths of the different layers are as follows :—

I.	0·09
II. & III.	0·38
IV.	0·26
V. & VI.	0·42

In the posterior part of its extent the motor area lies along the superior margin of the hemisphere. Anteriorly it descends on the lateral surface to reach the insular area and on the mesial surface as far as the intercalary subzonal sulcus, where it abuts on cortex of the calloso-marginal type.

The giant pyramidal cells are somewhat small, in conformity with the small size of the animal. The arrangement of the cells corresponds to the multilaminar type of group (*b*) described by Brodmann (1).

3. *Parietal Area.* (Pl. II. *a.*)

The cortex in this area is characterized by relatively deep zonal and pyramidal layers, and by a marked development of the inner

granular layer. The depth of the whole cortex averages 1·43 mm., and the depths of the various layers are as follows:—

I.	0·13
II. & III.	0·63
IV.	0·30
V. & VI.	0·36

The well-developed pyramidal layer should be noted and also the presence of some conspicuous large pyramids scattered in the infragranular layers. In contrast to the striate and Betz cell areas, the precise limits of the parietal area are difficult to define accurately. Anteriorly it meets the Betz cell area and posteriorly the striate area, but separated from the latter by a narrow band of cortex, in which the inner granular layer is not quite so distinctly differentiated and the pyramidal layer better developed. Below, the line of demarcation between the parietal and temporal areas is particularly vague, the transition between the two areas being rather a gradual change than an abrupt boundary. I feel confident, however, that the accompanying illustration represents the actual facts of the case as accurately as possible. On the mesial surface of the hemisphere, the parietal area reaches almost to the corpus callosum, separated, however, from the latter by a band of cortex of the calloso-marginal type, which becomes wider as traced forwards.

4. *Temporal Area.* (Pl. III. *a.*)

This area shows a fairly well-developed inner granular layer and an arrangement of pyramidal cells somewhat more regular than in the previous cortical areas.

The average depth of the cortex is 1·48 mm. The measurements of the various layers are as follows: -

I.	0·14
II. & III.	0·57
IV.	0·28
V. & VI.	0·48

The pyramid cells in the lamina ganglionaris are well developed and show an orderly and even formation, which assists considerably in the recognition of this area. At the lower part of the temporal region the inner granular layer is not so well developed, and somewhat larger cells are found in the ganglionic layer. This region possibly represents area 20 of Brodmann.

5. *Frontal Area.* (Pl. II. *c.*)

The average depth of the cortex in this area is 1·28 mm., and the measurements of the cortical layers are as follows:—

I.	0·15
II. & III.	0·38
IV.	0·29
V. & VI.	0·48

In this area the relative depth of the zonal layer is to be noted. The inner granular layer is particularly diffuse, so that it is difficult to define its limits. The absence of large cells in the ganglionic layer is also a characteristic feature. This area is limited posteriorly by the Betz cell area, the boundary between the two areas being comparatively easy to define, and the determinations of the boundary-line made by means of two series of sections of different specimens correspond closely. Anteriorly the area extends to the anterior pole of the brain. It has not been found possible definitely to subdivide the area further by variations in its cortical structure.

The extent of the frontal area as shown in the diagram is, perhaps, rather deceptive, for it must be remembered that the anterior pole of the cerebrum becomes considerably attenuated, so that the surface-area occupied by this type of cortex is not so large as it seems on casual inspection.

6. *Insular Area.* (Pl. I. *c.*)

This area is here so called rather because of the position which it occupies than of any suggestion of homology with the insular cortex of higher primates. It shows a well-developed inner granular layer which is somewhat diffuse, while the pyramidal layer is comparatively thin and contains somewhat small cells, and the infragranular layers are well developed. The average depth of the cortex in this area is 1·23 mm., and the depths of the various layers in the cortex are as follows :—

I.	0·13
II. & III.	0·41
IV.	0·24
V. & VI.	0·44

7. *Retrosplenial Area.*

This is a small localized area, characterized by an extreme development of the granular layer and absence of the lamina pyramidalis, and it clearly corresponds to the area retrosplenialis of Brodmann. It borders on the hippocampal formation, projecting backwards immediately below the splenium of the corpus callosum and extending down the neopallial margin as a thin band.

8. *Calloso-marginal Area.* (Pl. III. *b.*)

The cortex is characterized by the absence of a definite granular layer, and, practically speaking, three layers only are clearly recognisable—the lamina zonalis, lamina pyramidalis, and lamina multiforme. The anterior division of this area (8 *a*) shows a rather better-developed pyramidal layer than the posterior division (8 *b*). The distribution of these areas is shown in the accompanying diagrams. The two divisions are continuous over

70*

the upper surface of the corpus callosum, but here the area is
hidden for a short space from the surface and buried by the
great expansion of the striate area.

THE CORTICAL AREAS.

The correlation of these areas which I have found distinct in
Tupaia minor with the major divisions of Brodmann, described in
his works on cortical localization, is not difficult. The principal
points which may be remarked upon here are the extent of the
specialized visual cortex and the well-marked frontal area lying
in front of the Betz cell area. On the lateral surface the visual
cortex extends forwards almost to the mid-point of the superior
margin of the cerebral hemisphere, an extent which is considerable
when comparing it with the corresponding area of other mammals,
e. g., *Erinaceus* (Brodmann) and *Sciurus* (Fortuyn). On the
mesial surface, the expansion of the visual cortex is even more
evident, breaking up (superficially) the calloso-marginal area
into two separate parts by its extension to the corpus callosum.

The frontal area is well developed, though, as mentioned above,
its surface-extent is somewhat difficult to judge, by reason of the
attenuated form of the frontal pole of the cerebrum.

THE CEREBELLUM.

The cerebellum of *Tupaia minor* is of a simple generalized type,
and in its degree of complexity stands in an intermediate relation
to *Macroscelides* and *Tarsius*. In general shape it presents a
median antero-posterior elevation (the vermis), broader in front
than behind, and separated from two lateral lobes by shallow
depressions. Projecting on either side are prominent petrosal
lobes. The dimensions of the cerebellum are as follows:—

Antero-posterior, median line	8·5 mm.
Breadth of vermis (max.)............................	6·5 „
„ including lateral lobes	10·5 „
„ „ petrosal lobes.....................	15·5 „

The anterior surface of the cerebellum is hollowed out by the
prominent anterior corpora quadrigemina. Postero-superiorly,
the surface is markedly convex, and is divided into some 9 or 10
folia by transverse fissures which, in some cases, are continued
on to the lateral lobes. Viewed from the dorsal aspect, the
lateral lobes can readily be subdivided into the three areas, A, B,
and C as designated by Elliot Smith (4). Of these, area A
consists of one folium only, area B is divided into three in-
completely separated folia, while area C has four transversely
disposed folia. These areas are shown clearly in the figure.

Posteriorly the copula pyramidis is very distinct, connecting
the paraflocculus with that part of the median lobe which is
termed the pyramid. This band is slightly notched transversely

at its lateral extremity, though the degree of foliation of the copula appears to be somewhat variable in different specimens. The parafloeculus forms a prominent knob, divided by fissures into five or six folia. Immediately below it can be seen the flocculus, composed of a few small folia, the connection of which with the nodulus is not distinctly demonstrable macroscopically.

Text-figure 13.
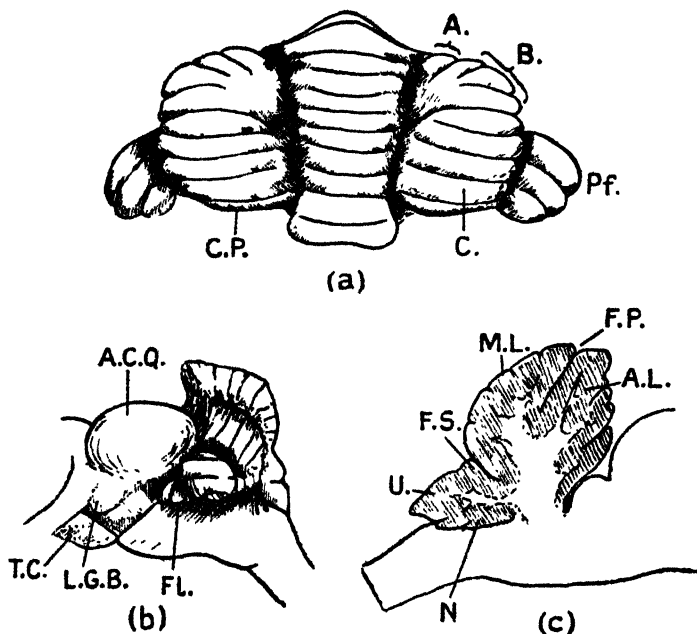
(*a*) Cerebellum, from postero-superior aspect. (For references not already given, see text.)
(*b*) Cerebellum, from lateral aspect. (The cerebral hemispheres have been removed.)
(*c*) Cerebellum, mesial sagittal section.

A.L. Anterior lobe.	L.G.B. Lateral geniculate body.
C.P. Copula pyramidis.	M.L. Middle lobe.
Fl. Flocculus.	N. Nodule.
F.P. Fissura prima.	U. Uvula.
F.S. Fissura secunda.	

(Other references as in text-fig. 1.)

The appearance of a median section of the cerebellum is shown in text-fig. 13, and its simplicity of structure is well shown by this illustration. It corresponds very closely with the figure of the cerebellum of *Erinaceus* as given by Elliot Smith. The weight of the cerebellum of *Tupaia minor* is approximately ·28 gram.

The Mid- and Hind-Brain.

The corpora quadrigemina are noteworthy for the large size of the anterior pair. The latter form conspicuous hemispherical eminences, measuring about 4·5 mm. antero-posteriorly and 5·25 mm. in width, hollowing out the occipital lobe of the cerebrum in front and the anterior surface of the cerebellum behind.

The posterior corpora quadrigemina are much smaller, forming transversely elongated bands, measuring about 1·75 mm. by 3·25 mm.

Text-figure 14.
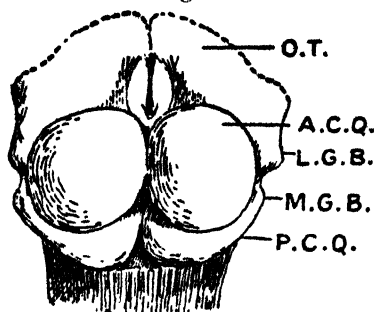
Mid-brain—dorsal view.

| L.G.B. Lateral geniculate body. | OT. Optic thalamus. |
| M.G.B. Medial　　　　„　　　　„ | |

(Other references as in text-fig. 1.)

Situated antero-laterally to the corpora-quadrigemina on the posterior aspect of the optic thalamus are the lateral and medial geniculate bodies, the latter of which are of inconspicuous size. On the ventral aspect of the hind brain can be seen the narrow pons, measuring approximately 2·5 mm. antero-posteriorly. Emerging from the pons at its lateral extremities are the large trigeminal nerves. Behind the pons is the broad corpus trapezoideum and, running down the ventral median line, the attenuated pyramidal tracts.

General Conclusions.

Carlsson, in a paper on the affinities of the Tupaiidæ (2), thus summarises the evidence afforded by the brain: "Das Gehirn bei *Tupaia* unterscheidet sich also von demjenigen der Insectivora und nähert sich demjenigen der höheren Säuger durch die Länge des Cerebrums, aber durch das kurze und gerade Corpus callosum zeigt es eine Übereinstimmung mit demjenigen der Insectivora."

The length of the cerebral hemisphere and the prominence of the occipital pole, due, at least in part, to the extent of the

visual cortex, is certainly striking in contrast with the brains of *Macroscelides* and the *Lipotyphla*. The relative size of the Corpus callosum in *Tupaia minor*, however, is not such as to indicate an approximation to the Insectivora. The brain of *Tupaia minor* is essentially primitive in its general formation, but it shows a reduction of the regions usually correlated with the sense of olfaction, and a corresponding elaboration of the visual apparatus which indicates a definite advancement from the conditions found in the Insectivora. Moreover, the visual cortex is remarkably elaborated and possesses a structure which, it is maintained, foreshadows the characteristic structure of the visual cortex found in the primates. The development and duplication of the inner granular layer of the visual cortex, which are so characteristic of the primate brain, are exhibited in an incipient form in *Tupaia* with a striking clearness, and the white line of Gennari, which is so marked in the brain of the Tree-Shrew, is also a primate feature.

There can be no doubt that, as Elliot Smith has quite recently reiterated in his essays on the Evolution of Man (6), the Tupaiidæ "display in the structure of their bodies positive evidence of relationship to the stem of the Primate phylum." The evidence for this has been put forward concisely and forcibly by Gregory (10), and corroborated by the researches of other workers (2) (3). The fundamental morphological differences between the *Menotyphla* and *Lipotyphla* have impressed certain systematists with the necessity of separating entirely these two groups of mammals. The suggestion is tentatively raised here that the evidence at hand points to a step further and indicates that the Tupaiidæ may logically be regarded as having attained a status which would justify their inclusion in the Primate phylum. The detailed evidence for this arrangement may be left to some future date, but it may be noted here that the primate features of the brain of *Tupaia* are paralleled in a very significant way by the evidence of the osteology, myology, vascular system and of the structure of the male and female genital system.

If this interpretation is correct, then the *Menotyphla* may be regarded as representatives of the most primitive group of Primates, and the nearest living representatives of the ancestral form from which was derived the whole of the Primate stem.

Note.—The microphotographs of the cortex of the brain were made for me by Miss Vaughan, of the Dunn Laboratory, St. Bartholomew's Hospital, and I wish to thank her for the care and patience which she has taken in this connection.

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EXPLANATION OF THE PLATES.

PLATE I.

A. Parietal cortex. (× 55.)
B. Motor cortex. (× 60.)
C. Visual cortex. (× 45.)
D. Visual cortex showing incipient duplication of the lamina granularis interna. (× 60.)

PLATE II.

A. Temporal cortex. (× 65.)
B. "Insular" cortex.
C. Calloso-marginal cortex. (× 60.)
D. Frontal cortex. (× 65.)

PLATE III.

A. Giant pyramidal cells from the motor area. (× 460.)
B. Endocranial cast of skull of *Tupaia minor*.
C. A sagittal section of the cortex at the junction of the Betz cell area and the frontal area. On the right the large pyramidal cells can be seen. On the left is the frontal area of cortex.

46. On Three new Acari belonging to the Superfamily Trombidioidea (Erythræidæ and Teneriffiolidæ). By STANLEY HIRST, F.Z.S.

(Text-figures 1–4.)

Family ERYTHRÆIDÆ.

FESSONIELLA, gen. nov.

Crista well-developed. A single eye on each side of the body. Fourth legs very long, the fourth and fifth segments strongly modified.

FESSONIELLA MITCHELLI, sp. n. (Text-fig. 1, Nos. 1–3 & 7.)

Colour (dry specimens) varying from pale stone-colour to pale grey ; ground-colour of legs pale yellow to deep brown ; both body and legs also clothed with minute silvery hairs. Body rather long-oval. Crista long; anteriorly it ends in a little mound beset with stiff hairs, and near the posterior end it widens to form a little oval structure bearing two very fine hairs ; posteriorly this oval structure is continued by a tongue-like strip of chitin. A single circular eye is present on each side of the body, and it has a well-developed convex lens. Hairs on body extremely numerous, those on the dorsum stiff and very minute ; hairs on the venter slightly longer and less stiff ; in the middle of the venter between the coxæ there are five pairs of comparatively long hairs. Genital slit long and narrow, being bordered with very minute hairs. Anal aperture narrow, but quite short; it also has a border of minute hairs, but they are somewhat longer than those of the genital aperture. Hairs on coxæ much sparser than on the venter. Penultimate segment of *palp* ending in a strong point and only furnished with fine hairs. *Legs* long ; the fourth, the longest, being about 1½ times as long as the body. Fourth and fifth segments of fourth leg curiously modified ; fourth narrow at the base, but wide distally ; fifth greatly swollen, being very wide and high, except at the base, which forms a short stalk ; the fourth leg is also smoother and shinier than the others, the modified segments having fewer hairs.

Length 2·2 mm.; greatest width 1·3 mm.

Loc. Table Mountain, Cape of Good Hope. Two specimens collected by W. Bevins. Both specimens were dry and glued on cardboard, but one has been mounted as a microscopical

preparation. The new genus and species of Erythræidæ described above differs from all other members of the family in the structure of its last pair of legs, the fourth and fifth segments

Text-figure 1.
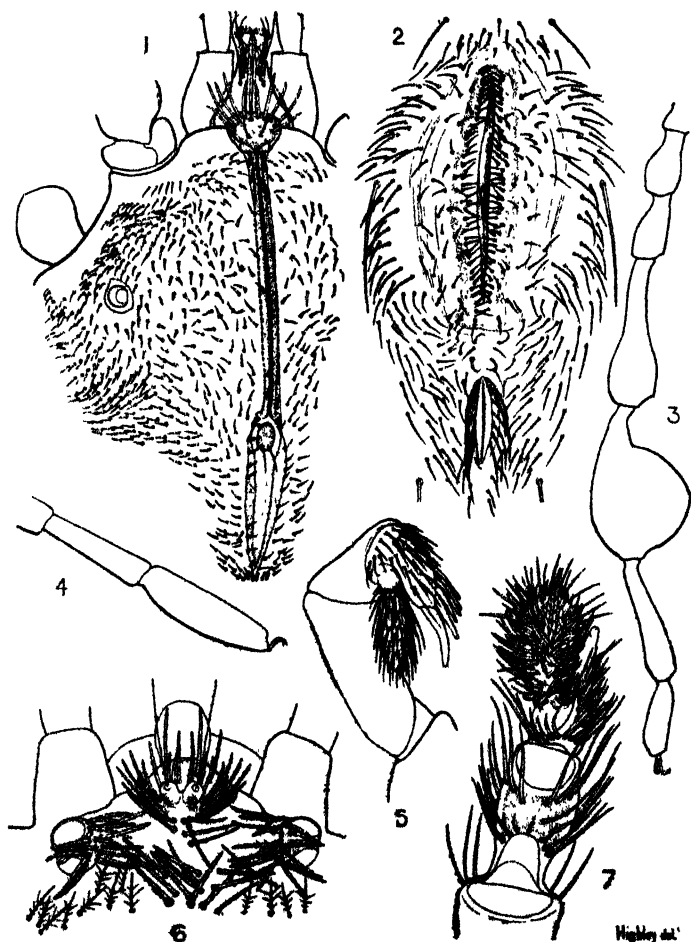
Fessoniella mitchelli, gen. & sp. n., ♀. (Nos. 1-3, 7.) No. 1. Crista. No. 2. Genital and anal apertures. No. 3. Fourth leg. No. 7. Palp.

Chyzeria novaezealandia, sp. n., ♀. (Nos. 4-6.) No. 4. Lateral view of metatarsus and tarsus of first leg. No. 5. Palp. No. 6. Crista and eyes.

of which are peculiarly modified (see Text-fig. 1, No. 3). I have named this interesting new species after Dr. P. Chalmers Mitchell, C.B.E., F.R.S.

CHYZERIA NOVÆZEALANDIÆ, sp. n. (Text-fig. 1, Nos. 4–6; text-fig. 2.)

Female.—*Body* much longer than wide. Anteriorly the cephalothoracic part has a little conical process projecting forwards above the base of the cheliceræ, but it is rather difficult to see. Behind this process is the *crista*, which is quite short, only consisting of a pair of rather eye-like tubercles scarcely separated at the base; a very long fine hair springs from each tubercle. These twin tubercles are surrounded by a cluster of stout bristles. There are two eyes on each side, and a cluster of bristles is placed on the inner side of each pair. *Five large and conspicuous dorsolateral processes* are present on each side of the abdominal part;

Text-figure 2.

Chyzeria novæzealandiæ, sp. n., ♀. Dorsal view of abdomen.

there is also a little median process at the posterior end, but it is ventral in position. A slightly raised crescentic structure also occurs on the surface of the dorsum near its anterior end, but it is not very distinct. Both plain stiff spines and also long and very fine feathered hairs are present on the processes; some of the plain spines arise from salient tuberculiform bases. Integument of middle of dorsum distinctly pitted. Genital opening large but wide, being rather short-oval; the anterior end of it is situated opposite the posterior end of the fourth coxæ. Anal aperture very much smaller than the genital one. Immediately behind each of the fourth coxæ there is a little projection very similar to

the dorso-lateral ones, but much less conspicuous. Hairs on venter mostly fairly fine and distinctly feathered.

Fourth segment of *palp* ending outwardly in a comb formed of six spines, the distal one being much stronger than the others. *Legs* of moderate length, each being furnished with a pair of smooth claws, those of the first leg considerably smaller than the claws of the other legs. First tarsus rather high, being about three and two-third times as long as high; posterior tarsi more elongated.

Length (not including capitulum) 2·8 mm.; greatest width 1·5 mm.

Habitat. New Zealand, specimens from Ben Lomond, Queenstown, and Routeburn, Otago (January 1914), T. Hall. (Chilton Coll.).

NOTE.—*C. ornata* Canestrini, the only species of the genus *Chyzeria* previously known, occurs in New Guinea. Judging by Canestrini's figures, his species differs in having three large anterior processes in the middle of the dorsum (whereas in *C. novæzelandiæ*, sp. n., there is only a slightly raised crescentic structure in that position), the crista differently shaped; lateral and posterior processes of abdomen curved, instead of being straight, hairs on coxæ and also spines on tarsus of palp fewer in number than in *C. novæzealandiæ*.

Family TENERIFFIOLIDÆ.

NEOTENERIFFIOLA, gen. nov.

Differing from *Teneriffiola* Strand and *Parateneriffia* Thor chiefly in having the coxæ of the legs much further apart, the fourth coxæ being widely separated from one another. Hairs on coxæ less numerous than in those genera. Third free segment of palp with a thumb-like process as in *Parateneriffia*.

NEOTENERIFFIOLA LUXORIENSIS, sp. n.   (Text-figs. 3 & 4.)

Female.—Body elongate-oval, being somewhat less than twice as long as its greatest width, and narrowed anteriorly; it is undivided, no distinct suture being present. Hairs on dorsum twenty in number (including the pseudostigmal ones), and they are distributed as shown in text-fig. 3. Anteriorly there are three pairs of hairs, not including the pseudostigmal ones; behind the eyes there is a transverse row of four hairs, the outer ones being long. There seems to be a slight transverse depression or furrow behind this row, perhaps representing the boundary between cephalothorax and abdomen. Behind this furrow there are four pairs of hairs forming a longitudinal series. All these hairs are rather stiff and provided with inconspicuous secondary hairlets. The pair of pseudostigmal hairs is placed behind the second pair

of ordinary hairs at the anterior end of the body; they are very
fine and arise from a curious stellate socket. Hairs on venter
few in number and distributed as shown in text-fig. 4. Hairs on
coxæ not very numerous; first coxa with four hairs, second with
three, third with four, and fourth with three. *Palp.* Fourth
(penultimate) segment of palp with two stout spinules placed near
the strong terminal claw. Fifth segment (tarsus) very small, and
furnished with eight hairs, two being very short, however.
Maxilla of palp with two pairs of stout spinules distally on its

Text-figure 3.
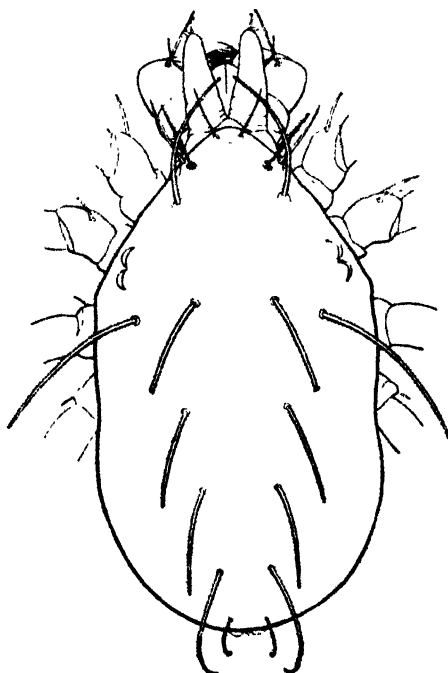
Neoteneriffiola luxoriensis, gen. & sp. n, ♀. Dorsal view.

ventral surface (one pair on each half) and also two longer setæ
near the base. Claws of anterior legs larger than those of the
posterior ones, each side of the claw is furnished with a comb
composed of numerous close-set small denticles; combs of posterior
legs very weak. The posterior legs have a short unpaired median
claw, but it is not present on the anterior legs.

Measurements in mm. Total length (including palpi) 1·07.
Length of first leg (excluding coxa) ·86; of second leg ·93; of
third leg 1·06; of fourth leg 1·34.

Habitat. Egypt; specimens collected by the author at Assuan (Jan. 1923) and at Luxor (March 1923).

Text-figure 4.
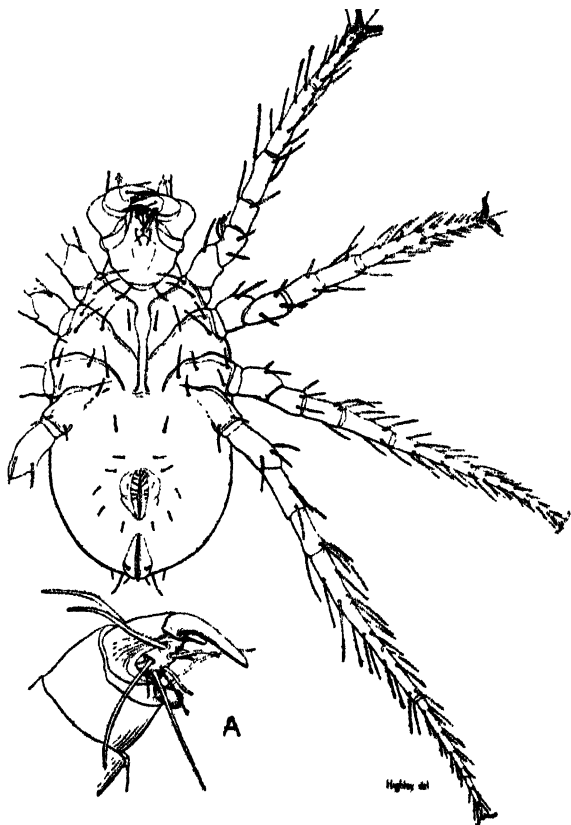
Neoteneriffiola luxoriensis, gen. & sp. n., ♀.　Ventral view.
A. Palp, greatly enlarged.

Note.—So far only two species of the family Teneriffiolidæ have been described, namely *Teneriffiola quadripapillata* Sig Thor, from Orotava, Teneriffe, in the Canary Islands, and *Parateneriffia bipectinata* Sig Thor, from Paraguay.　Hence the discovery of a new genus of this family inhabiting Egypt is of some interest.

1.

2.

REMAINS OF FEN BEAVER.

3

4   5.

REMAINS OF FEN BEAVER.

6

7
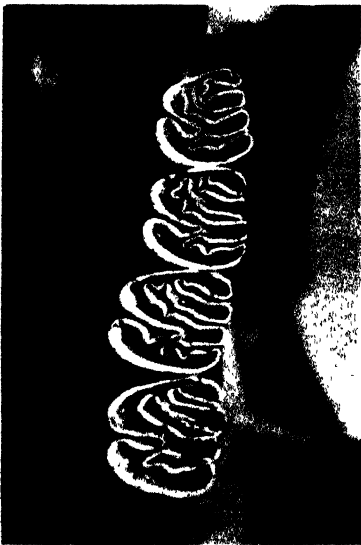
8.

REMAINS OF FEN BEAVER.

47. On the Remains of Fen Beaver in the Sedgwick Museum.—I. Skulls and Teeth. By Ivor Montagu, F.Z.S.

(Measurements in this paper are in millimetres throughout.)

(Plates I. III.*)

In certain circumstances a Beaver colony is situated in a forest pond of its own beginning. In others, maybe, as in the fen district, " it accommodated itself to the scrubby peat lands where woods were not available " †; finding the necessary expanse of nearly still water already present, and damming unnecessary, it had only to keep the water sufficiently clear of sedge. But in every case, however the essential familiar features of the Beavers' surroundings originated, the resultant pond, lodge, and so forth are constant. Indeed, the immediate environment of the members of any two Beaver colonies is, and probably was, very similar, irrespective of any lack of geographical or even temporal propinquity. It is not remarkable that this constancy of environment is paralleled by a constancy of form, and but little range of variation is seen in *Castor*, though the genus is widely spread over the whole Palæarctic and several thousand years.

The view that the Beaver was an animal of nearly constant characters was opposed by the work of Prof. Matschie‡, who recognized six separate recent species of *Castor* from Europe alone. This work was subjected to a destructive critical analysis by Dr. Forsyth Major §, who noticed in *C. galliæ* and *C. europæus* the award of independent value to synonyms, and in *C. balticus, C. vistulanus*, and Matschie's restricted *C. fiber* an overdue deference to variations in nasal measurement and tooth-pattern indicative only of age-differences. But Forsyth Major himself reaches the following conclusion : "The European Beaver ranges, or ranged, from Great Britain to Mongolia, and from Lapland to Spain (according to Strabo) and Italy. There is, therefore, every likelihood that more than one form will have to be distinguished in this vast region." And, again, in reference to Mr. Newton's identification of fossil Beavers from West Runton and East Runton with the recent European animal, he adds his expectation " that more complete specimens will reveal differences from the recent form or forms."

A careful examination of the skulls and teeth described in the
following paper, which form a fine series representative of some
thousand years of fenland, fails to reveal any differences, either
of shape or of dimension, of sufficient consequence to allow dis-
tinction to be drawn between them and those of the modern
European form *Castor fiber*. This is no remarkable fact, if the
generalizations at the head of this paper are to be accepted as
sound. Indeed, the acceptance of these generalizations weakens
the term "every likelihood," in Forsyth Major's conclusion.
Hitherto the systematics of the European *Castor* has been handi-
capped by the absence of a wide described series forming a
corpus sufficient to establish the nature of the normal skull at
various ages, and to determine the range of age and individual
variation that may occur in the enamel pattern of the teeth in
any one group. It was thus that Matschie so often attached
specific importance to single specimens and pairs, and, without
such a series, little certainty of their significance can attach to
any variations that may be described. Though of indefinitive
character, the following observations form a step towards the
assembling of the necessary corpus.

Material.

The material at present in the Sedgwick Museum comes from
upwards of seventy specimens. Of these, three are complete
skeletons, and in another twenty examples the skull is preserved
sufficiently to yield useful measurements. In nearly all skulls
sufficient teeth are present to assist in the preparation of a
summary of enamel variation. All the specimens are described
as having been extricated from the Cambridge fenland, and in
some instances a more precise locality and a date of finding is
available. There are no data by which to determine the relative
living dates of two given skulls, or, indeed, the place in time-
succession of any of the remains. If there had been discoverable
any wide range of variation in the remains, the absence of data
on this point would have handicapped the formulation of useful
conclusions. But, in view of the fact that the whole skull
material is so closely uniform, showing only differences to be
regarded as due to relative states of immaturity, one is justified
in making the inference that it represents a single persistent
form.

Skulls.

In the accompanying table are given the measurements of
fourteen complete or nearly complete skulls, the average of
twenty-two skulls (all those sufficiently entire to yield several
measurements, excepting a few young ungrown specimens), and
the maximum and minimum measurements in each dimension
considered.

C=condylobasal length, Zb = zygomatic breadth, Od = occipital depth, N = nasal length, Nn = breadth of nasals, D=diastema, Mn = mandible.

Mxt=maxillary cheek-teeth, Mnt = mandibular cheek-teeth.

	Cl.	Zb.	Od.	N.	Nn.	D.	M.	Mxt.	Mnt.
A.									
Burwell Fen, 1890	144·6	111·8	42·4	60 3	27·3	49·2	102	..	38
Strickland Collection, n.d.	143	102	42	64	28·5	49	...		
Burwell Fen, 1892	...	109·2		60·1	28	50· 3		34·8	.
Burwell Fen, 1912 ...	143	102·4	42·5	59·2	26·2	47	108·7	32 5	38
Swaffham Fen, 1905	143·5	110·5	41·3	60·4	28·4	47·8		32·5	..
Burwell Fen, 1913	143	106	..	59·5	27	48·5	102	33	38·5
Cambridge, n.d. . .	141	.	..	.	.	47·5	102	31·5	39·5
B.									
Cambridge, n.d.	141·5	106	42·5	...	..	46·5	100	32	36·3
Burwell Fen, 1906	141	106·5	41	54	26·2	44	96·7	32	35
Swaffham Fen, 1924 . .	139·3	104·5	41·5		.	45		33	...
Littleport, n.d.	139	105·5	40·2	59·7	28·4	45·3	98·5	32·5	35·8
Burwell Fen, 1907 . . .	137	101·4	39·5	57·3	26·8	46·5	97·5	32	36·8
Cambridge, n.d.	135	.	41		26	44	98	.	36
Swaffham Fen, 1921	134	109	39·5	57	26	43	96·7	...	34
Average of 22 specimens .	140·6	106	41·2	58·8	27·2	46·8	99·8	32·6	36·8
Maxima of „ „ ..	144·6	111·8	42·5	64	28·5	50·3	108·7	34·8	39·5
Minima of „ „ ..	134	101·4	39·5	53	26	43	93·5	31·5	34

The constancy of the skull is indicated by :

   i. The dimensions of individual skulls.

   ii. The nearness of the maximum and minimum measurements.

   iii. The fact that the average nearly coincides with the mean between the maxima and minima.

If the value 100 is given to each of maximum dimensions, the minimum dimensions are found to have the following values :—

   Cl=93, Zb=91, Od=93, N=83, Mn=91, D=83, M=86, Mxt=90, Mnt=86.

The twenty-two skulls may be divided into two groups, using as criteria a sum of the several characters regarded as youth and age characters, the general size, the state of the cheek-teeth, the length constancy of diameter of the incisors, and the development of the sagittal crest.   If the value 100 is given to each average measurement of the group of twelve older skulls *, then the averages of the group of ten younger skulls † have the following values:

   Cl=96, Zb=99, Od=97, N=93, Mn=96, D=93, M=93, Mxt=98, Mnt=94.

---

   * A in the table.   † B in the table.

It is clear from these two sets of percentages that the group of measurements N, D, M, Mnt, is proportionately more variable than the other measurements. But these former relate to the length of the snout and to the size of the lower jaw. The fact that these parts show a wider range of variation than the skull, as a whole, clearly confirms the view that they grow proportionately faster, and that in them a relatively small size is to be regarded as a young feature.

Pls. I.-III. Fig. 1.   Burwell Fen, 1912.   Lateral view.
                    2.   Burwell Fen, 1890.   Dorsal   „
                    3.   Burwell Fen, 1912.   Ventral   „
                    4.   Reach Fen, 1885.   Lower jaw.
                    5.   Reach Fen, 1885.   „   „
                    6.   Strickland Collection, n.d.   Dorsal view.

The specimens shown in Pls. I. & II. figs. 1–5 are adult specimens. They are resembled, except within the small margin of the measurements recorded, by all the other specimens except a few very small ungrown individuals and the Strickland skull. The sagittal crest of Burwell Fen, 1920 (Pl. I. fig. 2), does not reach quite as far as the posterior end of the zygomatic arch. In certain younger specimens it is a little less developed, in a few, such as Burwell Fen, 1912 (Pl. I. fig. 1), it reaches to the arch, but only in the Strickland specimen (Pl. III. fig. 6) is it so exaggerated. The Strickland skull shows also an angularity consequent on its great age.

Teeth.

In reference to plication of the enamel in Forest-bed forms, Forsyth Major says the molars are "considerably less plicated than in the latter species (C. plicidens), although slightly more so than is the rule in recent beavers." He adds "a moderate plication of the enamel occurs, however, in old specimens of the recent form." A plication, about equal in degree to that figured by Forsyth Major, is to be seen only in some five or six of the skulls in this collection. It does not seem possible to correlate its occurrence with the living age of the skull (the fact that all the teeth, as well as the lower jaw, of the Strickland specimen are unfortunately missing, handicaps the determination of this point). It is more likely, therefore, that the plication indicates age in time-succession, unless it is purely idiosyncratic.

"The pattern of enamel folding is essentially the same in all the teeth, three narrow re-entrant folds on one side, a single wider fold on the other; in the maxillary teeth the three folds are on the outer side, while in the mandibular teeth they are on the inner side" *; in the maxillary teeth the inner fold is situated between the first and second outer folds, in the mandibular teeth

* G. S. Miller, 'Catalogue of the Mammals of Western Europe,' p. 952, B.M. N.H., 1912.

the outer fold is situated between the second and third inner folds.

In the succeeding tables, the phrase " typical pattern " is used in reference to the arrangement of enamel quoted from Miller at the head of this section.   The phrase " typical pattern with islet " is used in reference to an arrangement in which the first and second inner folds coalesce, leaving an islet.

Forsyth Major noted in young individuals that the typical pattern is often split and irregularly insulated, and that occasionally this form persists in older examples.

The instance on which he commented occurred in m_3 of the upper jaw. The evidence in the appended tables, and the examination of many isolated teeth in this collection, indicates that here also this phenomenon of irregular insulation occurs in p and in m_3 in both the upper jaw and the lower jaw.   Furthermore, it seems also a young sign, but frequently persistent in older specimens and consequentially not diagnostic of living age.   But the " typical pattern with islet " seems in no way related to living age.   As in recent examples of *C. fiber*, it is the normal form of p and m_3 in the lower jaw; it also occurs in m_2 in about 50 per cent. of the specimens and less frequently in m_1.

Pl. III. Fig. 7. Burwell Fen, 1890. Teeth of right side of upper jaw.
                                        p, m_1, m_2, m_3. Typical.
Pl. III. Fig. 8. Cambridge Fen, n.d. Teeth of left side of lower jaw.
                                        m. Typical. p, m_2, m_3. Typical with islet.

Upper jaw.—Summary of fifteen nearly complete sets of adult teeth.

p.   Typical pattern 10 (fig. 7).   The first outer fold meets the inner fold 2.
                                    The second outer fold meets the inner fold 2.
                                    The third outer fold is enclosed, not reaching the outer edge of the tooth 1.
M_1. Typical pattern 15 (fig. 7).
M_2. Typical pattern 15 (fig. 7).
M_3. Typical pattern 8 (fig. 7).   *a.* The second and third outer fold coalesce, leaving an islet 3.
                                    As *a*, and the first outer fold meets the inner fold 2.
                                    As *a*, but the third outer fold is enclosed, not reaching the outer edge of the tooth 1.
                                    The second outer fold is prolonged to reach the inner edge of the tooth 1.

Lower jaw.—Summary of twenty-seven nearly complete sets of adult teeth.

p.   Typical pattern with islet 24 (fig. 8).   Typical pattern 3.
M_1. Typical pattern 20 (fig. 8).   Typical with islet 7.
M_2. Typical pattern with islet 16 (fig. 8). Typical pattern 11.
M_3. Typical pattern with islet 24 (fig. 8). Typical pattern 1.
                                               Typical pattern but islet split to form second small islet 1.
                                               Typical pattern with islet, but third inner fold enclosed, not reaching the inner edge of tooth 1.

EXPLANATION OF THE PLATES.

Plate I.

Fig. 1. Burwell Fen, 1912.   Lateral view.
   2. Burwell Fen, 1890.   Dorsal   „

Plate II.

   3. Burwell Fen, 1912.   Ventral view.
   4. Reach Fen, 1885.   Lower jaw.
   5. Reach Fen, 1885.   „

Plate III.

   6. Strickland Collection, n.d.   Dorsal view.
   7. Burwell Fen, 1890.   Teeth of right side of upper jaw.
   8. Cambridge Fen, n.d.   Teeth of left side of lower jaw.

48. The Larva and Pupa of an Indian Cassidine Beetle (*Prioptera decemmaculata* Boh.). By S. MAULIK, F.Z.S., F.E.S., and C. DOVER, F.E.S.

(Text-figures 1 & 2.)

The Larva.

The larva of *Prioptera decemmaculata* is flattened and elongate, broadest about the middle, narrowed anteriorly, more so posteriorly, and is 9–11 mm. in length. It is of a dark brown colour, with a median, longitudinal, dorsal white stripe on the first two thoracic segments; the ventral surface, except at the sides and five apical abdominal segments, is creamy-white. The *head* is quadrate, almost as long as broad, anteriorly produced, the sides slightly rounded. It is not covered with a dorsal shield as in the genus *Aspidomorpha*. This is a characteristic of the imago, and it would seem that all the larvæ of the Cassidinæ resemble the adult in the presence or absence of a dorsal shield. The upper surface is more or less flat, with a deep, median, longitudinal furrow, which meets in the centre another semicircular impression, the ends of which are outwardly directed. The area behind this is somewhat elevated, the antero-lateral margin with two large strongly-chitinised, and three smaller, ocelli. The anterior part enclosed by the ⋎ is declivous, and almost at right angles to the surface of the head. The clypeus is narrow, broader than long, with a single minute three-segmented process on each side, representing the antenna. The labrum is about twice as broad as long, convex posteriorly, sides rounded, anterior margin concave and very finely serrated. The mandibles consist each of a single piece with fine sharp teeth on the inner side. The labium is roughly triangular in outline, the anterior margin truncated, the posterior margin and sides rounded, with a pair of short, closely-set, two-segmented processes situated anteriorly, representing the labial palpi. The maxillary palpi are three-segmented, the basal segment twice as long as the second, the terminal one small and conical. The first *thoracic* segment is about twice as long as the second, and is more thickly set with tubercles than the remaining segments; it is broader than long, with two long spines antero-laterally, the inner straight, oblique, and about equal to the outer, which is slightly curved, a single upwardly curved spine postero-laterally, and another shorter spine between these on each side. These spines are distinctly serrated at the base, the serrations being most con-

spicuous on the side away from the head. The second and third thoracic segments are together as long as the first, and are not individually very much broader than the next abdominal segment. They bear on each side a minute straight spine placed anteriorly and also a larger, upwardly curved, postero-lateral one. The *abdominal* segments do not differ from each other very markedly in shape, but become gradually smaller and narrower towards the apex. The lateral margins are triangularly produced, with a single apical spine on each side, which on segments 1 to 6 are successively shorter, those on segments 7 and 8 being about three times as long with fine, short, setiform spines on either side, and are curved downwards. The processes which

Text-figure 1.
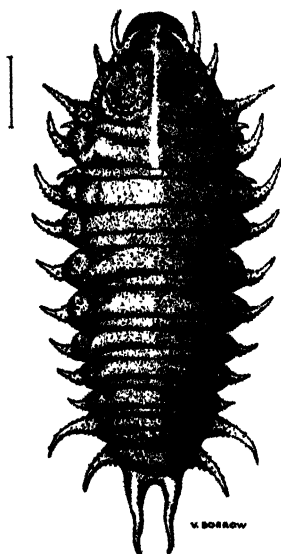
Dorsal surface of the larva of *Prioptera decemmaculata* Boh.

arise from the terminal segment, above the anus, which support the excremental structure made by the larvae of most Cassidinæ, one of us has proposed to designate the supra-anal projections. In this species there are two short, as compared to other species, supra-anal projections, gradually narrowed towards the apex, which are joined together at the base. There are altogether eight pairs of *spiracles*; each of the first seven abdominal segments bears a lateral spiracle on each side about the middle, while the first only of the thoracic segments bears a pair of spiracles, which are larger than those on the abdomen, and are situated postero-laterally. These spiracles are white, ringed on the outer side with brown. The *legs* are short and stout, and

are composed of three segments, the apical one bearing a well-developed and strong claw.

The larva of no species of *Prioptera* from the Indian region has hitherto been described, but Schultze (1908) has discussed the life-history of two species in the Philippines. The larva of *P. decemmaculata* may be separated from those described by Schultze as follows :—

Anterior spines on second and third thoracic segments developed only as short tubercles . . .	*P. sinuata* Ol.
Anterior spines on second and third thoracic segments triangular, distinct, but minute as compared with the posterior spines	*P. decemmaculata* Boh.
Anterior spines nearly as long as the posterior one . .	*P. schultzei* Weise.

The structure of the excremental filaments of the larvæ of certain Indian Cassidinæ has been discussed by Maulik (1919). In *P. decemmaculata* and the species described by Schultze, the filaments are short and stout, and arranged one above the other in two lateral bunches.

The Pupa.

The pupa is more or less ovate in shape, and is about 9 mm. in length. The head is covered by a dorsal shield which retains, to a certain extent, the larval characters, but the adult characteristic (viz., the explanate margin of the pronotum) is also present. The anterior edge is emarginate, each side of the emargination ending in a pair of spines. The whole of the upper surface is closely covered with minute, but distinct, tubercles, which are most crowded on the central area. Two fleshy triangular projections from the vertex of the head are visible, owing to the emarginate edge which leaves the head partly exposed. The edges of the pronotum are finely serrate, the posterior margin strongly sinuate. The anterior and posterior margins of the mesonotum, corresponding to the base of the pronotum, are strongly sinuate. The anterior margin of the metanotum is also sinuate, the posterior margin almost straight. The first three abdominal segments are of the same width, the lateral expansions of the first two large and broad and serrated at the sides, the spine on the third segment considerably smaller, those on the segments after this gradually reduced. There are four pairs of dorsal spiracles placed laterally on the first four abdominal segments. The general colour of the pupa is brown. The entire explanate margin of the pronotum including the anterior spines (the apices excepted), a median longitudinal line on the pronotum and a transverse line crossing it in the middle (where the white colour broadens considerably), and, finally, on each side of the longitudinal line, and posterior to the transverse one, two ill-defined, but more or less oval patches are dirty-white. The mid-dorsal area of the abdominal segments has a large dirty-white patch which is considerably reduced on the third segment and those after this. This white marking is longitudinally bisected by a brown line :

on the second tergite it is interrupted towards the sides by an oblique dark brown marking. The sides of the abdominal segments are of a darker brown than elsewhere. The underside, including the appendages, is of a creamy-white colour.

The material on which this note is based was collected by Mr. H. G. Champion in Almora, Kumaon, 4500 feet (August 1921), on *Premna barbata* Wall. (Verbenaceæ), and was entrusted to one of us (S. M.) through the courtesy of Mr. G. C. Champion.

Text-figure 2.
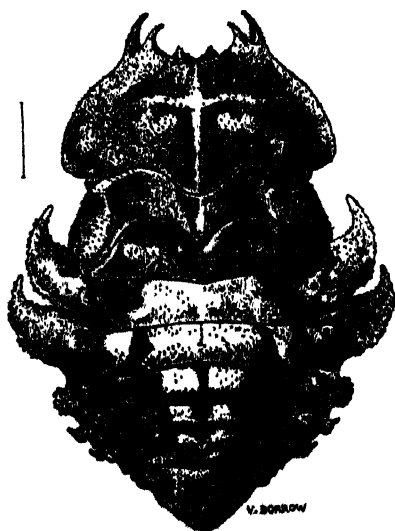
Dorsal surface of the pupa of *Prioptera decemmaculata* Boh.

The outline drawing of the larva has been made with the aid of the camera lucida from preparations made in the usual way by clearing in caustic potash, &c., and the pupa has been drawn direct from alcoholic specimens. The surface structure and markings of the larva and pupa have been very skilfully and accurately represented by Miss Violet Borrow, A.R.C.A., to whom our thanks are due.

References.

1908. Schultze, Philippine Journ. Sci. iii. p. 261 (*et seq.*).

1919. Maulik, Faun. Brit. Ind., Chrysomelidæ–Cassidinæ, p. 269 (*et seq.*).
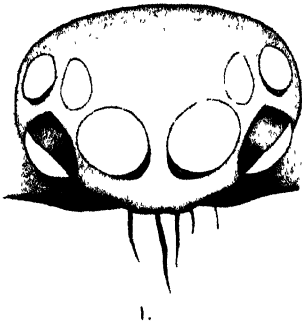
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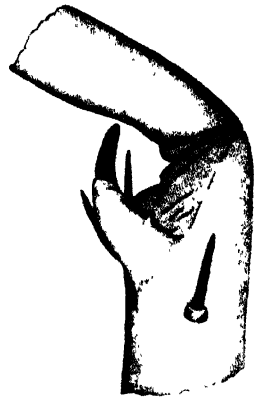
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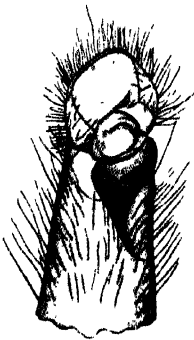
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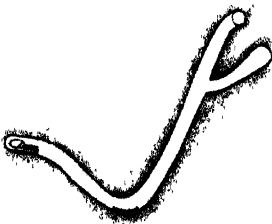
3.

b.

a

"back" entrance

↑ Edge of Log

ₓ ᵡₓ = food remains.

b.

4.

MYGALOMORPH SPIDERS FROM THE MALAY PENINSULA.

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5.

7

a.   6   b.   Fang

8

9.   b.   Fang

a.

MYGALOMORPH SPIDERS FROM THE MALAY PENINSULA.

10.

11.

12.

a. 13. b.

H.C.A.del.

John Bale Sons & Danielsson Ltd

MYGALOMORPH SPIDERS FROM. THE MALAY PENINSULA.

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14

15.

17

a. b.

16

A.

B.

a.

A. B.

b 18.

MYGALOMORPH SPIDERS FROM THE MALAY PENINSULA.

MYGALOMORPH SPIDERS FROM THE MALAY PENINSULA.

25

27.

a   26   b

a.   28.   b.
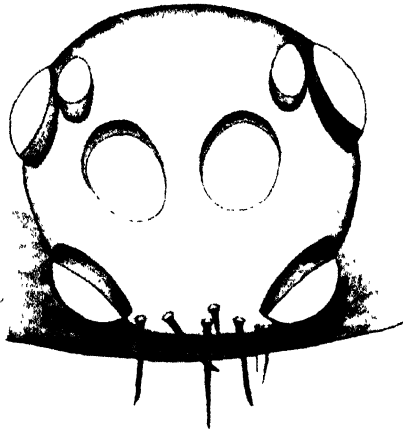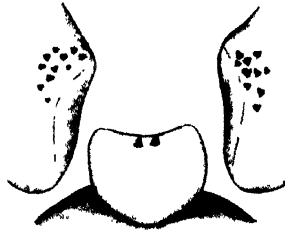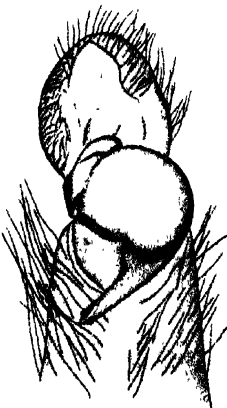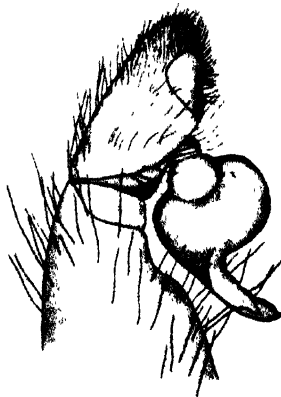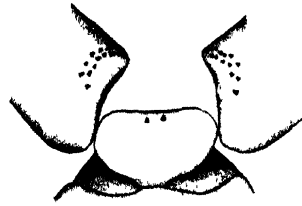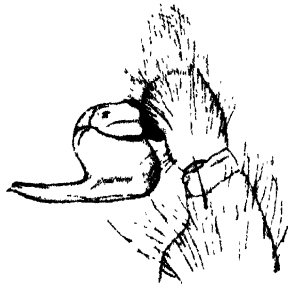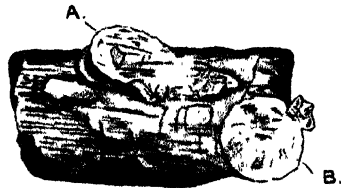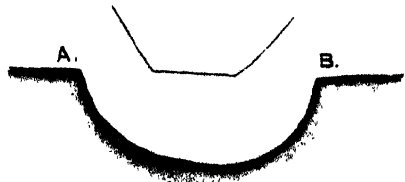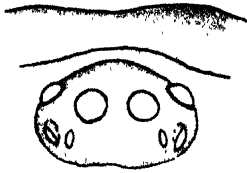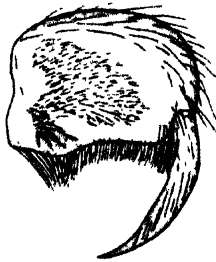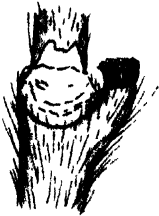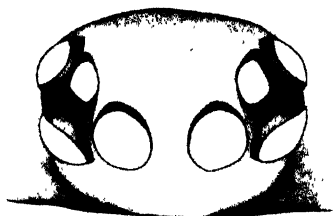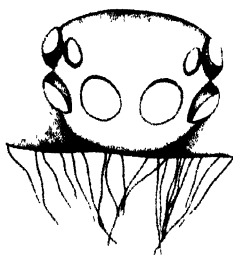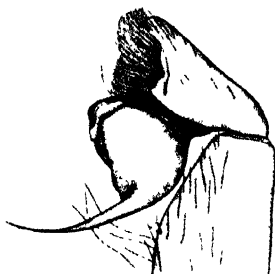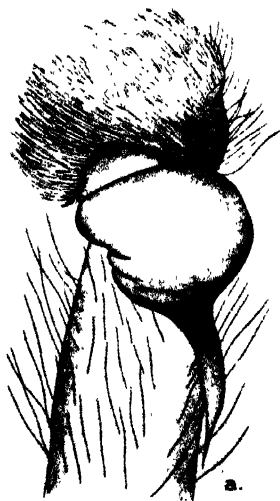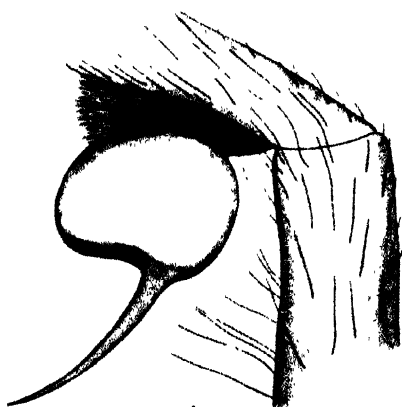
H C A del.

MYGALOMORPH SPIDERS FROM THE MALAY PENINSULA.

49. Some Mygalomorph Spiders from the Malay Peninsula. By H. C. Abraham, F.L.S., F.Z.S., F.R.G.S.

(Plates I.–VI.; Text-figures 1-3.)

The following notes and descriptions are the result of an examination of the Spiders of the sub-order MYGALOMORPHÆ contained in the collections of the Federated Malay States Museums and Raffles Museum, Singapore, as well as those which I have gathered together myself during the past four years.

The coloration of the spiders has, wherever possible, been given from living or freshly killed specimens; this has been indicated by "*Colour (L)*" at the head of the first paragraph of the description. "*Colour (S)*" implies that only spirit-specimens were available.

When the dentition of the margins of the fang grooves is discussed, the system adopted is that of numbering the teeth so that the one nearest the base of the fang is 1, the next 2, and so on in succession towards the base of the falx. This has been done because the teeth nearest the base of the fang are, in most cases, the largest and appear to be the most important.

In all cases, where the information is available, the exact localities, with altitudes, where different specimens were obtained have been given; and also, in italics and within brackets, the name of the collector, the date, and the collection to which the specimen belongs: *R.M.* indicating Raffles Museum, *F.M.S.* meaning F.M.S. Museum, and *A.* being my own collection *. As the highest point of Singapore Island is only just 500 feet above sea-level, no altitudes have been given for specimens collected there.

As might be expected in a region in which very little systematic spider-collecting has previously been done, the proportion of new species is high; the results may be tabulated thus :—

Total number of Species 14
New Species 6
Species of which the Males are here described for
    the first time 2

I wish here to express my gratitude to Mr. H. C. Robinson, Director, F.M.S. Museums, and to Major J. C. Moulton, O.B.E., late Director of Raffles Museum, for their kindness in placing the material in their respective collections at my disposal for

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* Thus: Penang Hill, 2000 feet (*Ridley, May* 1890, *R.M.*).

examination, as well as for help in many ways freely rendered at all times. My thanks are also due to the Director of the British Museum (Natural History) for allowing me access to the collections there and every facility for study: and to Mr. S. Hirst and his staff for their courtesy and help.

It will not, perhaps, be out of place to refer here to the great loss sustained by araneologists in general, and by myself in particular, by the recent death of Mr. H. R. Hogg, whose never-failing kindness and willingly tendered advice and help during the four or five years that I had been in correspondence with him, did very much indeed to foster and lead into right lines the interest which I had always taken in spiders.

Sub-Order **MYGALOMORPHÆ**.

Family A V I C U L A R I I D Æ.

Sub-Family CTENIZINÆ.

Group *AMBLYOCARENEÆ*.

Genus DAMARCHUS Thorell.

Thorell, Sv. Vet.-Akad. Handl. xxiv. No. 2, p. 14 (1891).
Simon, Hist. Nat. Ar. i. p. 107 (1892).
Pocock, Faun. Br. Ind., Ar. p. 169 (1900).
Simon, *op. cit.* ii. p. 900 (1903).

DAMARCHUS WORKMANII Thorell.   (Pl. I. figs. 1-4.)

Thorell, *loc. cit.* p. 15 (1891).
Workman, Malaysian Spiders, p. 81 (1892).

This species is very common on Singapore Island, and is represented in my collection by a large number of females and three males from this locality, as well as by a single male from Pahang.

Some of the larger females exceed considerably the measurement of the type as given by Thorell [*].

The male has not been previously found, and the following is its description :—

MALE.—*Colour (L)*. Cephalothorax and mandibles black, the former often with whitish 'bloom'; oral fringes reddish; labium, sternum, and coxæ dull brown inclining to orange posteriorly; legs and palpi, femora black with whitish 'bloom' as cephalothorax, other segments brown, palpal organ dark brown; abdomen dark brown thickly clad with long coarse black hair, opercula warm yellow, spinnerets dull brown.

Cephalothorax. Oval, truncate anteriorly and posteriorly, about ⅘ as broad as long, posterior margin about ⅔ the anterior. Thoracic fovea strongly procurved, deep, about ⅓ the width of the ocular tubercle.

_____

* *Loc. cit.* p. 17.

Eyes. Similar to those of the female; set on a tubercle which is about 1⅓ times as broad as long (Pl. 1. fig. 1).

Mandibles. Less powerful than those of the female; apex of falx with rastellus which is less conspicuous than that of female, being of smaller teeth and also masked by the long hairs of the anterior surface of the falx. Fang-groove with long thick fringes, and having the teeth of its inner margin smaller than in the female but similar in general arrangement.

Labium. About as long as the ocular tubercle and nearly 1¼ as broad as long. Armed with 2 or 3 minute teeth near apex *.

Maxillæ. The armament of teeth, which is so conspicuous in the female, is much reduced and the teeth themselves are minute.

Sternum. Nearly ¾ as broad as long and with its anterior margin half its greatest width. Clad with long black setæ.

Legs. Long and slender, those of the 4th pair (coxæ excluded) 3·8 times as long as cephalothorax (in female the 4th legs are 2·7 length of cephalothorax). Metatarsus+tarsus of 1st and 3rd pairs equal in length. Tibiæ of 1st pair armed at apex with a single long strong curved spur, situated on the inner side and projecting inwards and downwards (Pl. 1. fig. 2). The armament of spines is as follows:—

I. *Femora,* 1 internal sub-apical; *patellæ,* 1 internal subapical; *tibiæ,* an internal series of 2, 1 inferior sub-basal, 2 pairs inferiors (1 pair immediately at the base of the spur); *metatarsi,* 2 inferiors, 1 internal, 2 inferior apicals.

II. *Femora,* 1 internal sub-apical; *patellæ,* 1 internal subapical; *tibiæ,* an internal series of 2, an inferior series of 2, 3 inferior apicals; *metatarsi,* 1 pair internals, 2 inferiors, 2 inferior apicals.

III. *Patellæ,* an external series of 3; *tibiæ,* 1 superior, an internal series of 2, an exterior series of 2, an inferior series of 2, 2 inferior apicals; *metatarsi,* 1 superior, 3 internal superior, 3 external superior, inferior series of 3, 5 or 6 apical; *tarsi,* 1 external.

IV. *Tibiæ,* internal series of 2, 2 inferior apicals; *metatarsi.* internal series of 3, external series of 4, 6 or 7 inferiors, 6 or 7 apicals.

Scopulæ scanty on all tarsi, very slight on metatarsi I and II, lacking on metatarsi III and IV.

Tarsal claws armed with small teeth.

Palpi. 1¼ times as long as cephalothorax. Tarsus furnished with 2 fairly stout curved spines set, with their bases close together, on the superior surface of the segment near the commencement of the cleft (Pl. I. fig. 3 b). Bulb sub-oval, bi-lobed, with its long axis more or less parallel to tarsus and about 0·7 its length; short axis nearly ¾ long axis; the stem springs from the distal lobe, is thick at the base but becomes

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* These teeth are somtimes lacking; the female has 3–8 (generally 4) stout blunt teeth arranged, more or less definitely, in a transverse row.

slender and has a fairly sharp point—it curves slightly downwards and outwards and is about 1·2 times as long as the long axis of the bulb (Pl. I. figs. 3 *a* & *b*).

Abdomen. Oval, pointed anteriorly and posteriorly, nearly ½ as broad as long. Thickly clad with long hair.

Measurements (mm.) :—

MALE.

	Length.	Breadth.
Cephalothorax	7·5	6·1
Abdomen	7·1	3·4
Falx	3·4	—

Lengths of	Coxæ.	Tr. & fem.	Pat. & tib.	Met. & tar.	Totals.
Legs I	3·4	8·0	9·6	8·3	29·3
II	2·8	7·4	8·5	8·0	26·7
III	2·4	6·0	6·2	8·3	22·9
IV	2·5	8·6	9·1	11·2	31·4
Palpi	3·1	4·6	5·1	1·4	14·2

Superior Spinnerets : 1·3, 0·7, 1·1 = 3·1.

Habits, etc. The burrows of this species, which may be found plentifully in almost any roadside bank on Singapore and the adjoining islands (and probably also throughout the Peninsula), are silk-lined, 100 mm. to 250 mm. in length, and about 10 mm. in diameter. In almost every one that was examined, the lining was found to project very slightly (about 2 mm.) above the surrounding surface so as to form a sill of silk interwoven with sand, small leaves, etc.* The burrow appears to run in any convenient direction to suit the circumstances. In many cases it was found to be branched, the branch having no fixed direction or position with reference to the main tunnel and often being somewhat dilated at its distal end (Pl. I. fig. 4 *a*); in only one case was any sign of a door between the main burrow and the branch detected, and even in this case it was extremely doubtful as the burrow was damaged in digging it out.

The spider was usually found lurking at or near the inner end of the main burrow, and it was here also, in most cases, that *débris* of food, consisting of remains of cockroaches, beetles, and black ants, was found.

One specimen, found in a rotten log, had provided herself with a back way which was invisible from outside, being covered with part of the silk lining interwoven with moss, etc., and which remained closed by reason of the elasticity of the silk pulling its edges together (Pl. I. fig. 4 *b*).

Another burrow contained a sub-spherical cocoon about 9 mm.

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* This observation is at variance with that of Workman, who says (*loc. cit. supra*, p. 81; quoted by Thorell, *loc. cit. supra*, p. 17) : " *D. workmani* Thor. makes a simple tube in the ground about 3 inches deep, without any trap-door, and without raising the tube above the ground or in any way protecting it. . . ."

in diameter, in which were 63 newly-hatched whitish-yellow
spiderlings, each about 3 mm. long.

It would seem that the spiders are, in turn, preyed upon by
centipedes, etc., for in one burrow a large greenish centipede
was found which had apparently entered in search of the
rightful occupant.

There are two characters of this species which seem to
distinguish it from the rest of the genus: one is the presence
of a spine on the outer surface of the tarsi of the 3rd pair; the
other is the fact that the first 5 or 6 teeth on the inner margin
of the fang-groove are larger than the rest and are followed
by 2 which are set in towards the centre of the groove, the
remainder curving back to the edge, the effect being to give the
line of teeth (as seen in plan) a somewhat serpentine curve.

Locality. Singapore Island (*G. Hope Sworder & H. C. A.,
Oct.* 1922–*March,* 1923, *A.*); Pulau* Ayer Merbau & Pulau
Senang, near Singapore (*H. C. A., May* 1923, *A.*); Foothills of
Gunong Tahan, Pahang (1 male), 500–3500 feet (*H. M. Pendle-
bury, Nov.* 1921, *A.*); Pulau Tekong, near Singapore (*H. C. A.,
April* 1923, *A.*).

Previous records. Singapore Island (females only).

Specimens. Numerous females, 4 adult males. Type male in
B.M. (Nat. Hist.); other specimens, male and female, in
Raffles Museum; F.M.S. Museum, Kuala Lumpur; and my
own collection.

DAMARCHUS CAVERNICOLUS, sp. n.   (Pl. I. figs. 5–7.)

FEMALE.—*Colour* (*L*). Cephalothorax dark warm grey-brown,
mandibles darker; labium, sternum, and coxæ yellow-brown; oral
fringes red-brown; legs and palpi pale grey-brown, spines black;
abdomen, upper surface dark greyish red-brown mottled with
pale grey-brown forming a pattern of transverse interrupted
stripes, the mottlings being much larger and more distinct than
in *D. workmanii* Thor. and tending to run into one another,
underside dull yellow, the whole with a scanty coat of fine
down-lying hair.

Cephalothorax. 1¼ times as long as broad, very slightly shorter
than patella and tibia of 1st (or 4th) pair, distinctly shorter than
metatarsus and tarsus of 4th pair. Thoracic fovea well marked,
deep, strongly procurved; nearly ¾ as wide as ocular tubercle
and situated about ¼ the length of the cephalothorax from its
posterior margin. Caput high.

Eyes. Anteriors in a procurved line, medians slightly smaller
than laterals and about ¼ their own diameter from each other
and from their respective laterals; posteriors in a recurved line,
medians more pointed than in *D. workmanii* and with their
anterior edge level with the posterior edge of the anterior
medians. Posterior laterals and medians on each side close

* Pulau (*Malay*) = island.

together and the latter nearly touching the corresponding anterior median. Grouped together on a tubercle 2·3 times as wide as long and whose anterior edge is close to the front margin of the cephalothorax (Pl. II. fig. 5).

Mandibles. Falx just over ½ as long as cephalothorax, stout, strongly bowed anteriorly. Rastellus of slightly curved teeth, proportionately longer and more regularly placed than in *D. workmanii.* Fang-groove with 8 large pointed teeth which are not contiguous; order of size 3 or 4; 5, 6, 7 subequal; 1 and 8 subequal; the last about ½ the size of 3 or 4; the 5th is set in towards the mid line of the groove, producing a constriction in the latter. From the level of the 6th posteriorly to beyond the 8th tooth the groove is furnished with a number (about 28) of minute pointed teeth arranged in 3 anteriorly converging rows, the teeth of each row being about equally spaced and those of the outer row larger than the others *. Fringe of inner margin of groove scanty, of outer one fairly thick. Fang long and rather slender; strongly curved in distal half. (Pl. II. figs. 6 *a* & *b*.)

Labium. As wide as thoracic fovea and equal in length and width. Clothed with long setæ and furnished near apex with 1 to 3 stout teeth, the usual armament being 3 teeth arranged in an inverted triangle.

Maxillæ. Furnished with long setæ and with a number of stout teeth scattered over inner portion of the basal half.

Sternum. Slightly more than 1·3 times as long as wide and with its anterior margin not quite ¾ its greatest breadth. Posterior sigilla oblique, oval, not curved as in *D. workmanii.*

Legs. Those of 1st pair (coxæ excluded) nearly 3 times, those of 4th pair nearly 3½ times as long as cephalothorax. Patella and tibia of 1st pair taken together equal to same segments of 4th pair. Of 2nd pair, patella and tibia together are equal to metatarsus and tarsus together.

The legs are armed with spines as follows:—

I. *Tibiæ,* 1 inferior apical (internal), inferior series of 2 with 2 or 3 finer ones; *metatarsi,* inferior series of 2, 2 inferior apicals.

II. *Tibiæ,* inferior series of 3 or 4 (fine); *metatarsi,* inferior series of 2, 2 inferior apicals.

III. *Tibiæ,* external superior series of 2, internal series of 2, inferior series of 2 (fine), 2 apicals; *metatarsi,* external series of 3, 2 pairs superiors, 1 external sub-basal, 2 pairs inferiors, 4 inferior apicals.

IV. *Tibiæ,* 2 pairs inferiors (fine), 2 inferior apicals; *metatarsi,* 2 pairs superiors, internal series of 2, 2 pairs inferiors, 2 inferior apicals, external series of 2, 1 external subapical.

Superior tarsal claws with 4 or 5 small teeth.

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* In *D. workmanii* similar minute teeth also exist, but they are arranged irregularly from just posterior to 7th tooth to just posterior to 8th; there are 9 teeth on inner margin of fang-groove of which 7th and 8th are set in.

Tarsal scopulæ all slight; those of 1st pair divided; of 2nd, 3rd, and 4th pairs widely divided.

Palpi. Furnished with spines as follows:—

Tibiæ, 1 external, 2 pairs inferiors, 2 inferior apicals, 1 internal apical; *tarsi,* 1 pair inferiors about ⅓ length of segment from its apex *.

Tarsal scopulæ extend to bases of segments and are very widely divided.

Tarsal claws strong, falciform, with 5 small teeth on proximal half.

Abdomen. Oval, narrower anteriorly; rather less than 1½ times as long as greatest breadth. Scantily clad with fine hair. Superior spinnerets half the length of the abdomen, set widely apart (1½ times their basal diameter) and rather far back, almost level with the anal tubercle which, seen from below, appears between them. Inferior spinnerets slightly longer than median segment of superiors, each close behind and inside its corresponding superior, so that the inferiors are about 1¾ their basal diameter apart. Anal tubercle semicircular, thinly clad with long coarse hairs.

Measurements (mm.):—

FEMALE.

	Length.	Breadth.
Cephalothorax	5·4	4·3
Abdomen	6·6	4·5
Falx	3·0	—

Lengths of	Coxæ.	Tr. & fem.	Pat. & tib.	Met. & tar.	Totals.
Legs I	2·5	5·2	5·5	5·3	18·5
II	2·1	4·4	4·5	4·5	15·5
III	1·7	4·1	3·6	4·4	13·8
IV	2·3	5·6	5·6	6·6	20·1
Palpi	2·2	3·4	3·4	2·4	11·4

Superior Spinnerets: 1·4, 0·6, 1·3 = 3·3.

Habits. Constructs a silk-lined burrow in the bat-guano composing the floor of the cave in which the spider was found. The burrow is apparently simple (though, owing to the fact that they were numerous and close together, this cannot be stated as a certainty), about 200 mm. long, and running in obliquely but less steeply towards the inner end, as shown in the diagram (Pl. 11. fig. 7). They had no trap-door, but the entrance, which was usually situated on or near the crest of a slope, was provided with a small sill composed of small particles of guano woven into the silk lining.

From remains found in some of the burrows it would seem that the principal food of the spider is the cockroach *Leucophæa striata* Kirby, which is very abundant in the guano of the cave-floor.

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* *D. workmanii* has only 1, *D. oatesii* has 2 but not paired.

Locality. The Dark Cave, Batu Caves, Selangor, F.M.S.; 300 feet (*H. C. A., Dec.* 1921 & *Jan.* 1922, *A.*).

Specimens. 4 adult females, 13 immature.   Type in B.M. (Nat. Hist.), other specimens divided between Raffles Museum, F.M.S. Museum, and my own collection.

Note.—In the collection at the B.M. (Nat. Hist.) there is a number of females and immature (B.M. no. 98.2.10.7.12) of which the locality is given as "Selangor (in caves)" (*H. N. Ridley*). Three of these females are much larger than the largest of my specimens, and they differ in having the teeth on the labium apparently much more variable in number (1 to 7, with a tendency to be arranged in a group). Beyond this, however, I can perceive no structural difference and I have no doubt that they are of this species.

The principal measurements (mm.) of the largest of these specimens are :—

	Length.	Breadth.
Cephalothorax	9·5	7·5
Abdomen	11·3	7·1
Falx	5·6	—

Sub-Family BARYCHELINÆ.

Group *BARYCHELEÆ.*

Genus IDIOCTIS L. Koch.

L. Koch, Ar. Aust. p. 482 (1873).
Simon, Hist. Nat. des Ar. i. p. 125 (1892).
Hogg, P. Z. S. 1901, p. 242 (1901).
Simon, *op. cit.* ii. p. 914 (1903).

IDIOCTIS LITTORALIS, sp. n.   (Pl. II. figs. 8 & 9.)

FEMALE.—*Colour* (*L*). Cephalothorax dark brown-grey; mandibles darker; labium, coxæ, and sternum pale yellowish grey; oral fringes pale red; legs and palpi pale yellow-grey with scopulæ and ungual tufts grey; abdomen, upper surface dark brown-grey, ventral surface pale yellow-grey.

Cephalothorax. Oval, 1·3 times as long as broad, twice as long as tibia I, not so long as patella and tibia IV, breadth less than length of tibia IV; posterior margin slightly notched; clad with short recumbent hair. Caput high, steep at sides, with a median longitudinal series of long setæ extending from the ocular tubercle to the thoracic fovea, cephalic striæ well marked. Thoracic fovea straight, transverse, equal in width to ocular tubercle.

Eyes. Mounted on a low tubercle which is slightly broader than long, with numerous erect curved setæ between the eyes. Anterior eye-line strongly procurved, posterior straight (or only

slightly procurved). Anterior laterals close to anterior margin of cephalothorax and a little more than 1¼ their own diameter apart; anterior medians circular, ½ the diameter of the anterior laterals, separated from each other by their own diameter and the same distance from the corresponding anterior lateral; posterior laterals about equal in size to anterior laterals and each separated from its corresponding one by a space about equal to the diameter of the anterior median; posterior medians oval, ⅔ as broad as long, with long axis equal to ½ the diameter of the anterior laterals, situated close to the posterior laterals with their anterior margins about ¼ their own short axis from the nearest point of the corresponding anterior median (Pl. II. fig. 8).

Mandibles. Falx comparatively slight, ½ as long as cephalothorax; rastellus of a few (6 to 8) short, stout, slightly curved, sharp-pointed teeth in a single series. Fang-groove with comparatively slight fringes, that on inner margin scanty. Inner margin with 8 stout, somewhat forwardly-inclined teeth of which the order of size is 3, 4, 7, 2, 5, 6, 8, 1; 1, 2, and 3 are contiguous and the rest are separated and about equally spaced; the row forms a straight line (fig. 9 *b*). In the centre of the groove and extending from the level of the 7th tooth to just beyond the 8th is a single row of 5 minute conical teeth which are also inclined slightly forwards, the anterior being the largest and their size diminishing in succession posteriorly (Pl. II. figs. 9 *a* & *b*).

Fang moderately stout, curved throughout its length.

Labium. Rounded anteriorly, 1·6 times as broad as long, equal in width to ocular tubercle; unarmed but with long curved setæ on the apical portion.

Maxillæ. About ½ as broad as long, fairly densely clad with long coarse hair. Armed with 2 to 4 (usually 4) sharp, rather long, conical teeth in a single curved series along the basal margin. Fringe along the inner margin short and somewhat ragged.

Sternum. 1·5 times as long as broad; anterior margin slightly incurved and 0·7 the greatest breadth, antero-lateral angles forming blunt points, bluntly pointed posteriorly. Clothed with long coarse hair.

Legs. Order of length IV, I, II, III; those of 4th pair (coxæ excluded) nearly 3 times as long as cephalothorax; clad with longish coarse hair.

The armament of spines is as follows :—

I. *Tibiæ,* 1 internal, inferior series of 2, 1 inferior apical; *metatarsi,* 1 inferior apical.

II. *Tibiæ,* 1 internal, inferior series of 2 ; *metatarsi,* 1 inferior apical.

III & IV. *Tibiæ,* 4 inferior apicals (very fine); *metatarsi,* 6 to 7 apicals (inferior and laterals).

All the spines are fine.

Scopulæ of all legs extend to base of metatarsus and are all divided, those of 3rd and 4th pairs broadly.

Ungual tufts slightly longer than the tarsal claws, which are well curved, sharply pointed, and armed with 1 to 4 small sharp teeth.

Palpi. Armed with fine spines as under :—

Patellæ, 1 internal; *tibiæ,* 1 superior internal, internal series of **2, 5** inferior apical.

Tarsal scopula extends to base of the segment and is divided. Tarsal claw small.

Abdomen. Oval, rounded anteriorly and posteriorly, 1·8 times as long as broad. Clad with coarse recumbent hair. Superior spinnerets small, basal segment longer than the other two together, distal segment very small; placed about ½ their own basal diameter apart.

- Inferior spinnerets small and cylindrical, placed close together and each close to its corresponding superior.

Measurements (mm.) :—

FEMALE.

	Length.	Breadth.
Cephalothorax	4·4	3·4
Abdomen	4·2	2·3
Falx . ... 2·2	2·2	—

Lengths of	Coxæ.	Tr. & fem.	Pat. & tib.	Met. & tar.	Totals.
Legs I	1·6	3·5	4·1	2·8	12·0
II	1·4	3·4	3·6	2·4	10·8
III	1·3	2·8	2·8	2·5	9·2
IV	1·6	3·6	5·2	3·9	11·3
Palpi	1·6	3·2	2·6	1·5	8·9

Habits. All the specimens except one were found by digging in the mud at the roots of mangrove trees between high- and low-water marks. It would seem, therefore, that the spider must construct a retreat which it is able to close in some manner when the water rises above it. Five immature specimens were taken in a short tubular web-lined retreat, 47 mm. long, which was burrowed into the mud wall of a crab-hole and which appeared to have a trap-door of the wafer type. The specimen found on Pulau Semakau had a short tubular retreat, closed by a simple wafer-type door about 6 mm. in diameter with the hinge on its lower edge, in the crevices of the bark of a mangrove tree just below high-water mark ; it was very difficult to see by reason of its having a quantity of bark *débris* woven into it.

A specimen which was kept alive for a considerable time refused all food offered it until it was tried with a marine polychæte worm known to the Malays as ' puмpun,' which is found plentifully in similar situations to those from which the spiders were collected. On the introduction of the worm into its cage the spider approached it without hesitation, bit it, then

waited until the worm's struggles had abated a little, after which it devoured it at leisure. From this it would seem that the worm is the spider's natural diet.

Locality. Kranji River, Singapore Island (*H. C. A., Dec.* 1922, & *Jan.* 1923, *A.*); Pulau Semakau, near Singapore (*H. C. A., May* 1923, *A.*).

Specimens. 3 females, 5 immature. Type in the B.M. (Nat. Hist.).

Genus SIPALOLASMA Simon.

E. Simon, Hist. Nat. des Ar. i. p. 123 (1892).
Pocock, Faun. Br. Ind., Arach. p. 176 (1900).
Simon, *op. cit.* ii. p. 912 (1903).

SIPALOLASMA OPHIRIENSIS, sp. n.   (Pl. III. figs. 10–13.)

FEMALE.—*Colour (S).* Cephalothorax dark brown; mandibles a little paler; labium, maxillæ, sternum, and coxæ brown, the posterior portion of the sternum and the coxæ of the 3rd and 4th pairs being somewhat yellowish; legs and palpi like cephalothorax with dark brown hair; abdomen. upper surface dark warm grey-brown, thinly clad with fine pale brown hair, ventral surface somewhat paler, opercula and spinnerets yellowish; oral fringes reddish.

Cephalothorax. 1¼ times as long as broad, somewhat attenuate anteriorly and with its greatest width immediately behind the 2nd pair of legs (*i. e.*, a little in front of the thoracic fovea); convex with caput higher than thoracic portion which slopes down to the posterior margin. Thoracic fovea transverse, very slightly procurved (almost straight), well marked and slightly wider than the ocular tubercle. The whole thinly clad with fine hairs, especially along the ridges between the radial striæ, and with slight fringes of coarser curved hair along the lateral and posterior margins.

Eyes. Occupy a prominent subcircular tubercle rather more than ¾ as long as wide, which has its anterior margin close to that of the cephalothorax. Anterior and posterior margins of the tubercle each furnished with a group of long black curved erect bristles. Anterior eyes in a strongly procurved line, sub-equal, laterals 1½ their own diameter apart and about 1 diameter in front of the medians, which are rather less than ½ a diameter apart. Posterior eyes oval, the laterals about twice as large as the medians which are close to them on each side and about their own long axis away from the outer posterior margin of the anterior medians (Pl. III. fig. 10).

Mandibles. Fringes of fang-groove comparatively slight, the outer being the heavier; inner margin of groove with 11 or 12 large sharp conical teeth, the last two slightly separated from one another and from the rest which are contiguous; 4th and 5th are subequal and the largest, the 8th or 9th being the smallest. Fang long and stout, slightly curved throughout its length.

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Labium. Trapezoidal in shape, about as broad at apex as long and about $\frac{1}{3}$ as broad again at the base; length about $\frac{1}{3}$ the width of thoracic fovea and equal to that of ocular tubercle. Furnished with scattered coarse curved setæ which are longer at apex and armed on its apical margin with 2 blunt stout spinules or teeth (Pl. III. fig. 11).

Maxillæ. Basal margin hollowed and armed with 10 to 12 teeth, similar to those on the labium, arranged along it in 3 rather irregular curved series (Pl. III. fig. 11).

Sternum. Width $\frac{4}{5}$ length, anterior margin straight and in width equal to $\frac{1}{2}$ length of sternum; posterior margin notched for reception of coxæ of 4th pair; opposite each coxa of 3rd pair is a small marginal sigillum. Clad with scattered coarse black setæ which merge into fine bristles along the margins.

Legs. Those of 4th pair rather less than $1\frac{1}{4}$ as long as those of 1st pair (coxæ excluded). Somewhat sparsely clad with longish coarse dark brown hair and armed with spines as follows :—

I & II. *Tibiæ,* 1 internal apical ; *metatarsi,* 1 inferior apical.

III. *Tibiæ,* 1 internal apical, external series of 2 : *metatarsi,* 1 internal superior, 3 external superiors, 2 pairs of inferiors, 2 superior apicals, 3 inferior apicals.

IV. *Tibiæ,* 1 internal apical ; *metatarsi,* 3 external inferiors, 1 internal inferior, 2 internal superiors, 2 superior sub-apicals, 3 inferior apicals.

Tarsal scopulæ of 2nd pair narrowly, of 3rd and 4th pairs broadly divided.

Tarsal claws very stout and strongly curved, those of 1st and 2nd pairs with 2 teeth, those of 3rd and 4th pairs with 1 stout tooth.

Palpi. Clad similarly to legs with coarse hairs. Armed with spines as follows :—

Femora, 1 fine internal superior sub-apical; *tibiæ,* 4 to 6 internals more or less in 2 series, 3 or 4 inferior apicals.

Tarsal scopulæ broadly divided.

Tarsal claws very stout, strongly curved, with a single long stout tooth.

Abdomen. Oval, inclined to be pointed posteriorly, rather less than $\frac{3}{4}$ as broad as long. Clad with rather coarse short recumbent hair which becomes longer and more erect on the posterior parts.

Spinnerets close under anal tubercle ; superiors separated from one another by rather less than their basal diameter, with the basal segment rather longer than the 2nd and 3rd segments together and having its basal diameter (which is rather less than that at the apex) about $\frac{1}{2}$ the length of the segment; inferiors distinctly clavate with their apices rounded, about equal in length to 2nd segment of superiors and each one close up to its corresponding superior. Anal tubercle conical, projecting downwards between basal segments of superior spinnerets ; about equal in length to median segment of superior spinnerets and with basal diameter rather less than its own length. Somewhat scantily clad with fine hair.

MALE.—*Colour* (*S*). Cephalothorax dark brown with longish yellow pubescence; mandibles dark brown, paler at the base; labium, sternum, and coxæ yellow-brown; legs and palpi dark brown with long hair, scopulæ yellowish; palpal organ brown with a yellow patch on the anterior surface of the bulb; abdomen brown, thickly clad with long yellow-brown hair; opercula and spinnerets yellowish; oral fringes reddish.

Cephalothorax. Smaller than that of female and shorter in proportion to its width. In addition to the clothing of short black hairs there is the remains of a long pubescence, most marked on the caput.

Eyes. Similar to those of the female.

Mandibles. Much smaller and weaker than those of the female. Inner margin of fang-groove with 10 or 11 sharp conical contiguous teeth, of which the 2nd is the largest.

Fang similar in form to, but much less powerful than, that of female.

Labium. Similar in relative size and proportions to that of female, but in the only specimen available has only one tooth which, however, from its position, seems to be one of a pair of which the other member is lacking.

Maxillæ. As in female, but with the spinules at base smaller in size.

Legs. Generally similar to those of female, but much longer in proportion to the body. Tibiæ of 1st pair have on inner surface near the apex an apophysis consisting of two stout, sharply pointed spurs; the inferior one long and sharp, the superior short with a large blunt tooth at its base on the superior side (Pl. III. fig. 12).

Palpi. Tibiæ without spines on inner surface. Apex of tarsi very unequally divided. Bulb of palpal organ large with stout downwardly-curved compressed stem, about as long as the diameter of the bulb and ending in a blunt, somewhat rounded point (Pl. III. figs. 13 *a* & *b*).

Abdomen. Smaller than of female, about 0·6 as broad as long. Clad with longish hair. Superior spinnerets larger in proportion than is the case in the female.

Measurements (mm.):—

FEMALE.

	Length.	Breadth.
Cephalothorax	11·0	8·8
Abdomen	11·5	8·3
Falx	5·5	—

Lengths of	Coxæ.	Tr. & fem.	Pat. & tib.	Met. & tar.	Totals.
Legs I	4·7	8·4	9·6	6·2	28·9
II	4·3	8·2	9·1	6·3	27·9
III	3·4	7·2	8·1	6·3	25·0
IV	4·3	9·8	10·2	10·4	34·7
Palpi	4·2	6·2	7·2	3·5	21·1

Superior Spinnerets: 2·1, 1·0, 0·5 = 3·6.

MALE.

	Length.	Breadth.
Cephalothorax	9·6	8·7
Abdomen	9·1	5·7
Falx	4·3	—

Lengths of	Coxæ.	Tr. & fem.	Pat. & tib.	Met. & tar.	Totals.
Legs I	4·2	9·4	11·0	9·0	33·6
II	3·6	9·4	10·6	8·6	32·2
III	3·5	8·6	8·7	8·7	29·5
IV	4·0	11·6	. 11·7	14·3	41·6
Palpi	3·6	5·0	6·0	2·2	16·8

Superior Spinnerets : 2·3, 1·2, 0·4 = 3·9.

Locality. Mount Ophir (Gunong Keledang), Johore; no altitude recorded (*P. B., August* 1905, *R.M.*).

Specimens. 1 female, 1 male. The types, deposited in the B.M. (Nat. Hist.) *ex coll.* Raffles Museum.

SIPALOLASMA ÆDIFICATRIX, sp. n.   (Pl. IV. figs. 14–18.)

FEMALE.—*Colour* (*L*). Cephalothorax blackish brown; mandibles blackish; sternum, labium, maxillæ, and coxæ yellowbrown; oral fringes reddish; legs and palpi, femora brown, almost glabrous, the other segments dark grey-brown with slight coat of longish hair; abdomen, upper surface dark warm grey-brown with numerous, somewhat obscure, rather small pale spots *, scantily clad with fine hair; ventral surface pale brownish grey, opercula and spinnerets dull yellow.

Cephalothorax. Less than 1¼ times as long as broad, equal in length to metatarsus and tarsus of 4th pair together; distinctly attenuate anteriorly with caput well marked off by very pronounced striæ, which run from the thoracic fovea into the anterior lateral margin of the cephalothorax. Thoracic fovea well marked, transverse, slightly procurved (rather more so than in *S. ophiriensis*), and equal in width to the ocular tubercle. There are a few setæ behind the ocular tubercle and a median longitudinal series of longer ones from thence to the thoracic fovea; similar setæ are arranged along the thoracic striæ.

Eyes. Set closer together than in *S. ophiriensis*, the tubercle being almost exactly as long as wide. The posterior medians are triangular in shape (Pl. IV. fig. 14).

Mandibles. Fringes of fang-groove slight; inner margin of groove with 10 large conical separated teeth, of which the 1st is the smallest, the 3rd and 4th are the largest, and the rest subequal but diminishing slightly and regularly in size from the 5th to the 10th.

* These spots become much more conspicuous in spirit-specimens.

Labium. 1½ times as broad as long and rather less than the thoracic fovea in width. Clad with long curved setæ and furnished with 2 blunt teeth near the apex *, rather nearer the base than in *S. ophiriensis* (Pl. IV. fig. 15).

Maxillæ. Fringe along inner margin somewhat scanty; the teeth along the basal margin are 12 to 14 in number and are arranged more definitely in two rows than is the case in *S. ophiriensis* (Pl. IV. fig. 15).

Sternum. Squarish, the greatest width being rather less than the length; anterior margin about ⅔ the greatest width. Clad with setæ and bristles as in *S. ophiriensis.*

Legs. Those of 1st and 2nd pairs shorter in proportion to length of body than in the last species. The arrangement of the armament of spines is as follows:—

I. *Tibiæ,* 1 internal apical; *metatarsi,* 1 inferior apical.

II. As I, with the addition of 1 inferior sub-basal (at proximal end of scopula) on *metatarsi.*

III. *Tibiæ,* 1 internal apical, 3 or 4 finer inferior apicals; *metatarsi,* 3 inferior apicals, 2 pairs inferiors, 1 internal sub-apical, external series of 3, 1 pair superiors (about ⅓ up from base).

IV. *Tibiæ,* 1 internal sub-apical, 3 or 4 fine inferior apicals; *metatarsi,* 3 inferior apicals, 2 pairs inferiors, 1 internal sub-apical, 1 external sub-apical, external series of 3.

Tarsal scopulæ of 1st pair very narrowly, of 2nd pair narrowly, of 3rd and 4th pairs broadly divided.

Tarsal claws long and well curved with 2 stout teeth, the inner ones of 2nd pair which have 3 and inner ones of 4th pair which have 1 †.

Palpi. Furnished with spines as follows:—

Tibia, 4 inferior apicals, internal series of 2, external series of 2.

Tarsal scopulæ narrowly divided.

Tarsal claws stout, stoutly curved, with 3 stout slightly-curved teeth (increasing in size successively from proximal to distal) on basal half.

Abdomen. Oval, somewhat pointed posteriorly, nearly 1·3 times as long as cephalothorax and almost 0·8 as broad as long. Scantily clad with shortish hair.

Superior spinnerets rather close together, being separated by about ½ their basal diameter; rather less than 0·3 the length of the abdomen, with the basal segment slightly longer than the other two segments taken together.

Inferior spinnerets about equal in length to the median segment of the superiors, cylindrical, with their diameter about ½ their length, placed close together behind and between the superiors.

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* But see note on labial teeth p. 1108.

† These figures apply to the type-specimen ; the number of these teeth is, as is generally the case, subject to variation.

MALE.—*Colour* (*L*). Cephalothorax dark brown with long whitish-yellow hair; mandibles dark brown; labium, sternum, maxillæ, and coxæ brown; legs and palpi dark yellow-brown, thinly clad with longish fine black hair; abdomen dark warm brown with long dark brown hair; opercula greenish, the posteriors edged with dark orange; spinnerets yellowish; oral fringes red.

Cephalothorax. Flatter and broader than that of female (about 1·1 times as long as broad). Thoracic fovea slightly wider than ocular tubercle.

Mandibles. Much less powerful than those of the female, but with armament of inner margin of fang-groove similar.

Labium. About $1\frac{1}{2}$ times as broad as long, slightly narrower than ocular tubercle. Armed near apex with 3 teeth in a transverse, slightly curved line.

Sternum. Greatest width about equal to length; anterior margin $\frac{1}{2}$ the greatest width.

Legs. The tarsi of the 1st pair are furnished at their apices each with 2 stout curved spurs of which the inferior is the larger and is curved upwards and forwards, the superior one, not quite so large, being curved downwards and inwards and having at its base a blunt tooth not so large as in *S. ophiriensis* (Pl. IV. fig. 16). The armament of spines is as follows:—

I. *Tibiæ*, 2 externals, 1 internal immediately below the spurs; *metatarsi*, 1 inferior sub-basal.

II. *Tibiæ*, 2 inferior apicals, internal series of 3; *metatarsi*, 1 inferior sub-basal.

III. *Tibiæ*, 3 inferior apicals, 1 internal sub-apical, external series of 2; *metatarsi*, 3 inferior apicals, 2 pairs inferiors, external series of 4, 2 internal superiors.

IV. *Tibiæ*, 2 inferior apicals, 2 externals, 1 internal sub-apical; *metatarsi*, 3 inferior apicals, 5 inferiors, 4 external superiors, 2 internal superiors.

Tarsal claws of 1st pair with 3, of 2nd and 3rd pairs with 2 teeth, and of 4th pair with 1 tooth.

Tarsal scopulæ not so thick as in female; of 1st and 2nd pairs narrowly, of 3rd and 4th pairs broadly divided.

Palpi. Tibiæ with their inferior surfaces bare, but having a fringe of long hairs (setæ) along each margin; not furnished with spines. Tarsi divided into two very unequal portions but the bifurcation not very evident.

Palpal organ with bulb spheroidal, its short axis about $\frac{3}{4}$ the long one; stem stout, slightly compressed, nearly straight, about as long as the short diameter of the bulb and terminating in a blunt point (Pl. IV. figs. 17 *a* & *b*).

Abdomen. Slightly shorter than the cephalothorax and rather less than $\frac{3}{4}$ as broad as long. Clad with long shaggy hair.

Spinnerets as in the female.

Measurements (mm.) :—

FEMALE.

	Length.	Breadth.
Cephalothorax	8·0	6·7
Abdomen	10·4	8·2
Falx.........	4·2	—

Lengths of	Coxæ.	Tr. & fem.	Pat. & tib.	Met. & tar.	Totals.
Legs I	3·2	5·4	6·2	4·5	19·3
II	2·8	5·6	6·1	4·6	19·1
III	2·5	5·2	5·5	5·0	18·2
IV	2·1	7·1	7·4	8·0	25·3
Palpi . ..	3·0	4·1	5·1	2·5	14·7

Superior Spinnerets : 1·6, 0·9, 0·6 = 3·1.

MALE.

	Length.	Breadth.
Cephalothorax	7·7	6·8
Abdomen	6·7	4·7
Falx	2·8	—

Lengths of	Coxæ.	Tr. & fem.	Pat. & tib.	Met. & tar.	Totals.
Legs I	2·9	8·0	8·8	8·3	28·0
II	2·7	7·6	8·5	8·0	26·8
III .	2·5	6·7	6·8	7·3	23·3
IV ...	3·2	9·8	9·9	12·2	35·1
Palpi ...	2·5	4·5	4·8	1·8	13·6

Superior Spinnerets : 1·2, 0·6, 0·4 = 2·2.

Nest. A good-sized chamber of silk very cunningly concealed externally with rotten wood, etc. It has two doors of the wafer type, the hinges being always inwards, so that the doors open back to back. The nests collected were all found on fallen logs and generally in crevices on the lower portions, where they would be somewhat sheltered from the weather; the " back " door sometimes opened into hollows in the log and sometimes into the open air. The largest one taken measures 40 mm. between the outer edges of the two doors, the diameter of the doors being about 18 mm. (Pl. IV. fig. 18).

Habits. Most of the females and a number of immature specimens were taken in nests as described above, and when disturbed endeavoured to escape through the " back " door ; if the latter were held shut the spider tried to evade capture by holding the " front " door tightly shut from within, and so strong was its grip that quite a considerable amount of force was required to open the door. The immature male was taken under one of the logs on which the nests were afterwards discovered, whilst the mature male was found on a path in another part of Singapore Island. One female was taken whilst I was digging in a bank in an endeavour to follow up the burrow of a specimen of *Damarchus workmannii* Thor., but its nest was not observed.

A very young specimen was captured by a native collector, who stated that it had a small nest on the trunk of a rubber-tree.

It seems probable that the spider is largely, if not entirely, nocturnal in its habits, and the *débris* found near the nests appears to indicate that its principal diet is a large species of black ant. The apparent scarcity of males might be accounted for on the supposition that the females stick fairly closely to their nests whilst the males roam about (this is, of course, a well-known feature of the lives of several of the burrowing Mygalomorph spiders).

Locality. Singapore Island, females, imm. male, and juv. (*G. Hope Sworder & H. C. A., June, July, and August,* 1922, *A.*); (*n. c., April* 1923, *A.*).

Specimens. 5 adult females, 1 adult male, 1 imm. male, 8 juv. Types, male and female, in B.M. (Nat. Hist.); other specimens, females and immature, in Raffles Museum, F.M.S. Museum, and my own collection.

Note on Labial Teeth. An examination of the entire series of females and immature specimens shows that the number of labial teeth is not altogether constant, as 3 of the immature specimens and 1 adult have each only 1 tooth; this would also go to show that the variation is not attributable entirely to age.

Sub-Family AVICULARIINÆ.

Group ORNITHOCTONEÆ.

Genus MELOPŒUS Pocock.

Selenocosmia Simon, Act. Soc. Linn. Bord. xi. p. 161 (1886); (ad part. *S. albostriata*).

Melopœus Pocock, Ann. Mag. Nat. Hist. (6) xv. p. 179 (1895); id., Faun. Br. Ind., Arach. p. 205 (1900); Simon, Hist. Nat. des Ar. ii. p. 945 (1903).

MELOPŒUS MINAX Thorell.

Thorell, Ann. Mus. Civ. Genova, xxxvii. p. 182 (1897).
Pocock, Faun. Br. Ind., Arach. p. 205 (1900).

The collection of the F.M.S. Museum contains three females of this species.

Locality. Peninsular Siam; no altitude recorded; (*n. c., July* 1916, *F.M.S.*).

Previous records. Tenasserim.

Genus LAMPROPELMA Simon.

Simon, Hist. Nat. des Ar. i. p. 151 (1892); ii. p. 946 (1903).

LAMPROPELMA VIOLACEOPEDES, sp. n.   (Pl. V. figs. 19–24.)

FEMALE.—*Colour* (*L*). Cephalothorax dark brown with paler pubescence; mandibles the same with the setæ on anterior

surface brown and the external scopulæ black; oral fringes red; sternum and coxæ almost black with brown setæ, the former being provided with a close velvety covering of hair; labium and maxillæ dark brown; legs and palpi, dorsal surface similar to cephalothorax with pale brown long coarse scattered hairs, ventral surface a rich blue-violet when viewed at certain angles (the intensity of this colouring appears to vary in different individuals and is almost entirely lost, in all observed cases, just previously to moulting); scopulæ, dorsal surface pale golden brown, ventral surface dull grey-yellow with iridescent greens and blues; abdomen dark brown with obscure darker longitudinal median and oblique lateral stripes and with paler long hairs scattered over its surface, ventral surface blackish.

Cephalothorax. Ovate, squarely truncate anteriorly and with a median notch in the posterior margin; 0·9 as broad as long and ⅓ as wide across the anterior margin as at the level of the thoracic fovea. Rather flat, the cephalic region not markedly elevated above the thoracic. Clad with short recumbent hair, which is longer in the striæ (elsewhere it appears to be arranged in irregular tufts), and having a fringe of long curved coarse hair along all its margins, the anterior fringe being the more scanty and the posterior the thicker. Thoracic fovea shallow, transverse, very slightly procurved (practically straight), about ⅓ the width of the ocular tubercle; immediately anterior to it is a shallow longitudinal depression.

Eyes. On a transversely oval tubercle, which is rather more than ½ as long as wide and which has a group of 6 longish backwardly curved setæ on the mid-line between the anterior median eyes and the front margin and a single short seta between the anterior medians. The anterior eye-line is procurved as seen from above, the eyes being subequal and about equally spaced; the medians are circular and the laterals oval, about twice as long as wide. The posteriors form a straight line, the laterals immediately posterior to the anterior laterals and about the short axis of the latter away from them; the medians are each close to the corresponding lateral; the laterals are oval, similar in shape to, but somewhat smaller than, the anterior laterals; the medians, which are white and probably nocturnal, are longitudinally lenticular, rather less than ½ as wide as long, with their long diameter rather less than that of the posterior laterals and the space between them 4 times their long axis (Pl. V. fig. 19).

Mandibles. External surface of falx (Pl. V. fig. 20*a*) provided with a thick scopula, which merges at its lower basal angle into a stridulating apparatus consisting of 4 long, stiff, pointed, recumbent spines, which occupy a marked depression in the surface. These spines decrease in length from the anterior to the posterior, are flattened, and have their margins fringed with short hairs, the flat surfaces being striate (fig. 21). Fang-groove with long fringes, the inner margin being also armed with about 18 teeth, of which the first 5 are considerably larger

than the rest, which are small, except the last and last but two, which are about the same size as the 3rd; the order of size of the first five is 2, 3, 5, 1, 4 (fig. 20 b). Posterior portion of the groove granulate. Fang stout, strongly curved towards the apex, with lower margins lightly keeled throughout their length, the inner keel being the stronger; lateral surfaces with numerous curved striæ originating about quarter-way down from apex and merging into inferior margin just short of the base.

Labium. Rectangular, rather more than ¾ as long as wide, slightly hollowed at apex, with numerous long erect curved setæ and the apical surface thickly armed with small blunt spinules.

Maxillæ. Fringe along inner margin thick and long. Ventral surface furnished, on the inner portion, with numerous spinules similar to those of the labium. Inner surface has, above the suture, a thick tuft of pointed hairs in which are concealed a few pointed spines; below the suture is a slight fringe of pale recumbent hair and 11 short stout anteriorly-directed conical spinules ('tubercles,' Simon, Hist. Nat. des Ar. ii. p. 945) arranged more or less in two longitudinal rows. Apical margin furnished with about 5 long forwardly-pointing stout setæ set just below the suture (Pl. V. fig. 22).

Sternum. Squarely truncate anteriorly, rounded posteriorly; about 1·2 times as long as its greatest breadth, which occurs between the coxæ of the 2nd and 3rd pairs; anterior margin rather more than ½ greatest breadth. There is a pair of small sigilla on the line of greatest breadth, each sigillum being about halfway between the lateral margin and the mid-line.

Legs. Long and slender, those of 1st pair being the stoutest. Order of length I, IV, II, III. Unarmed, except for a "comb" of 7 to 9 very fine black spines on the apical margins of all the tibiæ and small paired lateral spines near the apices of the metatarsi of 3rd and 4th pairs*.

Ungual tufts very dense and silky, projecting just beyond the claws. Scopulæ very dense, projecting about the diameter of the tarsus on either side of the segment.

Tarsal claws stout, strongly curved, unarmed; set closely together.

Palpi. Femora with fringe along each margin of ventral surface, that along inner margin being much less prominent than the other. Patellæ and tibiæ with apical "combs" similar to those on tibiæ of legs.

Tarsal scopulæ thick, undivided, and projecting about ½ the diameter of the segment on each side.

Tarsal claws stout, strongly curved, unarmed; normally hidden in the ungual tuft.

Abdomen. Oval, about ⅔ as broad as long.

* Thus differing from the diagnosis of the genus (based on a single species, *L. nigerrimum* Simon) given by M. Simon in Hist. Nat. des Ar. i. p. 151.

Superior spinnerets about 0·4 the length of the abdomen, slender, separated at their bases by a space about equal to $\frac{1}{4}$ the length of their basal segment.

Inferior spinnerets immediately below superiors, about $\frac{1}{4}$ their length and $\frac{1}{2}$ their own length apart.

Anal tubercle small and conical, basal breadth about twice its length.

MALE.—*Colour* (*L*). Cephalothorax brown, thickly clad with long recumbent hair, which is longest in the striæ and forms a long curved fringe along all the margins; mandibles dark brown with dense yellowish hair arranged in 3 longitudinal bands; scopula yellowish; oral fringes reddish; fangs red-brown; labium, maxillæ, coxæ, and sternum clad with yellow hair; legs and palpi brown with yellow hairs and very slight indications of the violet coloration on the ventral surface; abdomen, dorsal surface yellow-brown, ventral surface paler, the whole clad with long hair.

Cephalothorax. Similar to that of the female, but more densely pubescent and with the marginal fringes longer. The depression anterior to the thoracic fovea is wanting or, at all events, is much less strongly marked and masked by the hair.

Eyes. Similar to those of the female.

Mandibles. Differ from those of the female in having only 13 teeth on the inner margin of the fang-groove; these are more widely spaced and the first 4 are much larger than the rest, their order of size being 2, 3, 1, 4.

Labium. Rather more hollowed at the apex than is the case in the female.

Sternum. Anterior margin about 0·7 the greatest width.

Legs. More slender than those of the female. Tibiæ of the 1st pair have each, on the inner surface near the apex, a blunt apophysis in the form of a flat cushion thickly covered with fine sharp stiff spines and with a single stouter spine arising from the distal side of its base and projecting obliquely forward (Pl. V. fig. 23).

Palpi. Tibiæ armed with a single stout spine on the internal surface near the apex and have also on the outer surface, about $\frac{1}{4}$ up from the base, a small dark brown blunt projection *. Tarsi divided almost equally at apex by a deep cleft. Bulb of palpal organ sub-spherical; the stem outwardly-curved, compressed, and terminating in an oblique blunt point (Pl. V. figs. 24 *a* & *b*).

Abdomen. Spinnerets set more closely together than in the female, the superiors being separated by about $\frac{1}{2}$ the length of their basal segment whilst the inferiors are sub-contiguous.

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* This projection, however, does not exist in two other males collected since the above was written (August 1928), and it would therefore appear that its presence in the type-specimen is accidental.

Measurements (mm.):—

FEMALE.

	Length.	Breadth.
Cephalothorax	21·5	20·2
Abdomen	24·4	15·7
Falx	10·0	—

Lengths of	Coxæ.	Tr. & fem.	Pat. & tib.	Met. & tar.	Totals.
Legs I	10·0	27·1	28·9	24·0	90·1
II	8·2	24·0	26·1	22·1	80·4
III	6·8	20·1	20·4	20·4	67·7
IV	7·6	23·5	25·1	24·0	80·2
Palpi	9·4	17·3	18·4	9·1	54·2

Superior Spinnerets: 4·3, 2·7, 2·3 = 11·3.

MALE.

	Length.	Breadth.
Cephalothorax	19·3	18·2
Abdomen	19·5	11·5
Falx	10·2	—

Lengths of	Coxæ.	Tr. & fem.	Pat. & tib.	Met. & tar.	Totals.
Legs I	9·3	28·2	32·8	28·7	90·0
II	8·8	26·0	28·6	26·7	90·1
III	7·4	22·4	23·7	24·4	77·9
IV . . .	7·3	25·4	28·3	29·6	90·6
Palpi	9·0	20·7	24·4	4 3	58·4

Superior Spinnerets : 3·2, 2·4, 4·1 = 9·7.

Habits. The specimens on which observations have been made have all been collected in mangrove swamp, and have in every case been found to be inhabiting hollow Nyiereh trees (*Xylo-carpus moluccensis* M. Roem), the hole being lined with a thin but strong sheet of silk.

Some of the females which were kept in captivity (two were kept for over 5 months) were very aggressive and struck on the least provocation, and, in the case of one of them, a sound, like the very faint hiss of a serpent, always accompanied the act of striking. It was also observed that when the spider was provoked the violet coloration on its legs and palpi became much more intense and was very conspicuous on account of the 1st and 2nd pairs of legs being raised up. The intensification of the colour is possibly due to movement of the hairy covering of the limbs. They fed voraciously, taking a large grasshopper almost every day and only occasionally refusing food for two or three days. When about to moult they completely covered the mouth of their hole with a sheet of web similar to that with which it was lined.

From the fact that the type male was collected on Penang Hill at an altitude of about 2000 feet, it seems that the species

is not confined to the mangrove belt, as I had at first thought likely, but probably lives in any locality where it can find suitable trees. The apparent confinement of the species, on Singapore Island, to the mangrove belt would be accounted for by the lack of other large jungle on the island.

Localities. Penang Hill (Belle Vue Bungalow), about 2000 feet (type male) (*Dr. G. D. Freer, Oct.* 1899, *R.M.*): Labis, Johore, no altitude (*F. G. Whitehead, Aug.* 1914, & *J. S. Willes, Sept.* 1911, *R.M.*): Pulau Bulang, Riau Archipelago (*Mrs. de Burgh Thomas, Oct.* 1921, *A.*); 3rd Mile Estate, Seremban, no altitude (*R. G. Sherar, July* 1923, *F.M.S.*); Kranji River, Singapore Island (*H. C. A., Feb. to April* 1923, *A.*); ? loc. (? *coll.,* ? *date,* *F.M.S.*).

Specimens. 10 adult females, 3 adult males, 2 immature. Types, male and female, deposited in B.M. (Nat. Hist.); other specimens in Raffles Museum, F.M.S. Museum, and my own collection.

Simon (Hist. Nat. des Ar. ii. p. 946) suggests that his genus *Lampropelma* is possibly synonymous with Pocock's *Phormingochilus*; the sternum of the present species is not nearly so sharply narrowed anteriorly as is shown in the figure of that of *P. everettii*, Pocock (Ann. & Mag. Nat. Hist. (6) xv. 1895, pl. x. fig. 4 *a*). The form of the scopula and stridulating apparatus on the external falx appears to agree more nearly with that of *Melopœus albostriatus* Simon, as depicted by Simon (Hist. Nat. des Ar. ii. p. 944, fig. 1090), than it does with that figured by Pocock of *P. everettii* (*loc. cit.* pl. x. fig. 4 *b*). The dentition of the fang-groove of the present species appears to be very similar to that of *P. everettii*; the legs, however, are much longer in proportion to the size of the body.

Group SELENOCOSMIE 1.

Genus SELENOCOSMIA Auss.

Selenocosmia Ausserer, Verh. z.-b. Ges. Wien, 1871, p. 204; Pocock, Ann. & Mag. Nat. Hist. (6) xv. p. 170 (1895).
Phrictus L. Koch, Arach. Aust. p. 488 (1874) (*nom. praeocc.*).
Phlogius Simon, Bull. Soc. Ent. Fr. (6) vii. p. cxcv (1887).
Selenocosmia & *Phlogius* (ad part.), id., Hist. Nat. des Ar. i. p. 146 (1892).
Psophopœus Thorell, Ann. Mus. Civ. Gen. 1897, p. 175.
Selenocosmia & *Phlogiellus* Simon, *tom. cit.* ii. p. 955 (1903).

SELENOCOSMIA INERMIS (Auss.).

Ischnocolus inermis Ausserer, Verh. z.-b. Ges. Wien, xxi. p. 185 (1871).
Phlogiellus atriceps Pocock, Abh. Senck. naturf. Ges. xxiii. pt. 4, p. 595 (1897).
Selenocosmia inermis, Hirst, Rec. Ind. Mus. iii. p. 384 (1909).

My collection contains 5 adult females and 3 immature specimens, which I refer to this species, as they agree with Ausserer's description and the specimens in the British Museum (Nat. Hist.) in everything but size—nine being the larger.

They had web-lined burrows in banks, 150 mm. to 250 mm. long and about 10 in diameter, with a " sill " of silk interwoven with grass-stems, etc.; in one or two cases a loose flap of this silk formed a rudimentary door, but these occurrences were probably accidental.

The measurements (mm.) of the largest of my specimens are as follows:—

FEMALE.

	Length.	Breadth.
Cephalothorax	11·2	8·6
Abdomen	11·0	7·0
Falx.........	7·5	—

	Lengths of	Coxæ.	Tr. & fem.	Pat. & tib.	Met. & tar.	Totals.
Legs	I	5·3	10·5	11·6	9·5	36·9
	II	4·3	9·0	9·5	8·9	31·7
	III	3·5	8·0	7·8	9·3	28·6
	IV	4·2	10·6	11·3	13·0	39·1
Palpi	....	5·1	7·7	7·9	4·5	25·2

Superior Spinnerets : 2·0, 1·5, 2·1 = 5·6.

Locality. Singapore Island (*H. C. A. & n. c.* 10/2/23, *A.*).
Previous records. Java and Sumatra.
Specimens. 5 adult females and 2 immature; these have been divided among Raffles Museum, F.M.S. Museum, and my own collection.

SELENOCOSMIA JAVANENSIS (Walck.).

Mygale javanensis Walck., Hist. Nat. des Ins. Apt. i. p. 216 (1837).
M. monstrosa C. L. Koch, Die Arachn. v. p. 14 (1839).
Eurypelma monstrosa id., Uebers. d. Arachn., Syst. 5, p. 73 (1850).
Mygale javanensis Dol., Tweede Bijdr. &c. p. 4 (1859).
Selenocosmia javanensis Auss., Verh. z.-b. Ges. Wien, xxi. p. 204 (1871).

The three collections contain a number of females and one male of this species. Those collected by myself were found in web-lined unbranched burrows about 500 mm. long and 50 mm. in diameter, running obliquely downwards into banks, usually with one or two turnings in them; there was no attempt at a door of any sort, but one of them had a leaf fastened over the entrance in the manner of a verandah—probably an accidental occurrence. The *débris* found in the burrows included remains of black ants, millipedes, small beetles, and in one instance of snail-shell.

Several varieties of this spider have been described, but, in most cases, the distinctions between them appear to be so slight that they will prove, in all probability, to be merely individual ones; some of them, such as the area occupied on the internal surface of the maxillæ by the stridulating apparatus, seem to be quite feasibly explained by difference of age of the specimens.

Localities. Various parts of the Malay Peninsula including Singapore Island.

Previous records. Java and the Nicobar Islands.

Specimens. 11 females, 1 male, 2 imm. The male is in the collection of the F.M.S. Museum.

SELENOCOSMIA TAHANENSIS, sp. n.   (Pl. VI. figs. 25 & 26.)

MALE.—*Colour.* Cephalothorax blackish brown (hairs have been rubbed off); mandibles the same with long dull yellow hair; sternum, labium, and coxæ dull yellow-brown; oral fringes reddish; abdomen dull greyish yellow with a close coat of longish hair, opercula yellowish: legs and palpi brown, basal halves of the femora darker than the other parts of the appendages.

Cephalothorax. Ovate, somewhat attenuate anteriorly, about equal in length to metatarsus and tarsus of 3rd pair taken together and about 0·8 as broad as long. Convex, the cephalic portion decidedly elevated. Thoracic fovea strongly procurved, well-marked, equal in width to ocular tubercle (also equal in width to labium).

Eyes. Anteriors in a straight line, the laterals slightly smaller than the medians. Posterior line recurved; laterals oval and about ½ as wide as long, their long axis about 0·8 the diameter of the anterior medians, situated behind the anterior laterals and separated from them by about ½ their own long axis; medians placed midway between posterior laterals and anterior medians, ovate, about 0·6 as wide as long, and about 0·6 as long as posterior laterals, white (Pl. VI. fig. 25).

Ocular tubercle very high, about 0·8 as long as broad, situated close up to the anterior margin of the cephalothorax.

Mandibles. Falx normal in shape; stridulating bristles on external surface numerous and setiform; fringe on external margin of fang-groove thick, of long hair; on inner margin sparse; the inner margin of fang-groove armed with 10 fairly large, pointed, subequal, separated teeth; posterior portion of groove indistinctly granulated. The group of recumbent spines on the inner surface of the falx is nearer the upper basal angle than is usually the case.

Fang strongly curved with a fine sharp point.

Labium. Half as broad again as long; the breadth equals that of thoracic fovea or ocular tubercle. Clad with longish curved hairs and the apex thickly, finely spinulose.

Maxillæ. About 0·4 times as broad as long, with the basal portion of under surface finely spinulose and with a thick long fringe along internal inferior margin. Bacillar area on the internal surface ovate in shape, about 0·6 as wide as long, more pointed anteriorly than posteriorly (where its margin is almost straight), its lower edge reaching to the base of the fringe (actual measurements 1·7 mm. long, 1·0 mm. wide). The bacilli are comparatively large and bluntly pointed.

Sternum. About 1·25 as long as greatest width, but somewhat attenuate anteriorly, so that the anterior margin is only 0·6 of the greatest width.

Posterior sigilla oblique, about width of labium apart and rather less than half that distance from the margin.

Legs. Long and slender. Order of length (coxæ excluded) IV, I, II, III. Metatarsus and tarsus (taken together) of 2nd or 3rd pairs equal to length of cephalothorax; patella and tibia of 1st pair taken together longer than corresponding segments of 4th pair. Legs of 4th pair (coxæ excluded) just over 3·7 times as long as cephalothorax.

Legs unarmed, except for metatarsi of 3rd and 4th pairs, which each have 5 apical spines.

Tarsal scopulæ of 4th pair distinctly divided.

Palpi. Long and slender, patella and tibia, taken together, being equal to corresponding segments of legs of 4th pair. Tarsus unequally divided, and from the base of the cleft issues the bilobed bulb from which projects the long, slender, finely-pointed, outwardly-curved stem (Pl. VI. figs. 26 *a* & *b*).

Abdomen. Rather more than half as broad as long. Superior spinnerets a little more than half as long as abdomen, very slender, with their bases separated by a space equal to the length of their median segment. Inferior spinnerets behind and between superiors, about ½ as long as the distal segment of the superiors and about ½ their own length apart.

Measurements (mm.):—

MALE.

	Length.	Breadth.
Cephalothorax	8·5	7·1
Abdomen	9·5	5·2
Falx	5·2	—

Lengths of	Coxæ.	Tr. & fem.	Pat. & tib.	Met. & tar.	Totals.
Legs I	4·0	9·5	11·7	9·8	35·0
II	3·4	8·5	9·2	8·6	29·7
III	3·0	7·1	7·3	8·5	25·9
IV	3·4	9·4	10·4	11·5	34·7
Palpi	3·7	8·1	10·3	1·8	23·9

Superior Spinnerets : 1·8, 1·3, 1·8 = 4·9.

Locality. Foothills of Gunong Tahan, Pahang; between 500 and 3500 feet (*H. M. Pendlebury, Nov.* 1921, *A.*).

Specimens. A single male, the type, which has been sent to the British Museum (Nat. Hist.).

This spider appears to be very closely related to *S. raciborskii* Kulcz.* from Java. The present species differs in having the palpi relatively longer (especially the patella and tibia taken together); the stem of the palpal organ longer, more slender, and more curved; and the superior spinnerets longer.

Genus COREMIOCNEMIS Simon.

Phlogius Simon, Ann. Soc. Ent. Fr. 1892, p. 279 (ad part. *P. cunicularius*).

Coremiocnemis Simon, Hist. Nat. des Ar. i. p. 146 (1892); id., *op. cit.* ii. p. 956 (1903).

COREMIOCNEMIS VALIDUS Pocock.   (Pl. VI. figs. 27 & 28.)

Pocock, Ann. & Mag. Nat. Hist. (6) xv. p. 175 (1895).

The collection of the Raffles Museum contains 10 females and 1 male of this species. All these females, except two, are remarkably uniform in colour and characters, and conform exactly with Pocock's description; of the two exceptions, one specimen has the setæ on the legs arranged more definitely in series than is the case with the other specimens, the other appears to differ slightly in the relative proportions of the various segments of the legs but, as it is rather badly damaged, no definite conclusion can be arrived at and I have somewhat doubtfully referred it to the present species.

The inner margin of the fang-groove of the females is armed with 13 to 16 (usually 14) teeth, of which the 5th (or 6th) is small and the rest large.

Egg-cocoons. In the same jar with a series of six of the females were included four dirty-white spheroidal egg-cocoons about 32 mm. in diameter and 18 mm. thick; each one has one or two pieces of grass woven into it like a stem. One was opened and found to contain 125 newly-hatched young, maize-yellow in colour and about 4·3 mm. in total length. The "skin" of the cocoon is tough and fairly thick, but there appears to be a total absence of any flocculent silk within. There is, unfortunately, no record of the position in which the cocoons were found or whether each came from a separate burrow.

As the male of this species has not previously come to light, I herewith append its description.

MALE.—*Colour* (*S*). Cephalothorax and mandibles blackish with dull yellowish pubescence; labium and maxillæ brown with dull yellow hair; sternum and coxæ dull yellow, the former with brown sigilla; oral fringes reddish; legs and palpi dull yellow with dorsal surface of femora light brown; abdomen pale dull

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* Kulczynski, Bull. Int. Akad. Krakow, 1908, p. 537.

yellow-brown, more brown on anterior portion; palpal organ dark brown.

Cephalothorax. Similar in shape to that of female, but much more hairy (the ocular tubercle is especially so) and the marginal fringes more strongly marked.

Eyes. Similar to those of the female (Pl. VI. fig. 27).

Mandibles. Similar in form to those of the female, but having the hairs on the anterior and dorsal surfaces of the falces longer and denser. The stridulating setæ on the external surface are finer than in the female.

The fang-grooves of the single specimen show quite a large variation in the number of teeth on the inner margin: the right-hand one has 10 teeth with the 2nd the largest and the 10th the smallest, whilst the left-hand one has 13 teeth with the 1st small, the 2nd much larger, the 3rd the largest, and the 13th a little larger than the 1st. The posterior half of the gooove is granulate. The fang is rather more slender and more curved than in the female.

Maxillæ. Stridulating rods finer and hair on inner surface coarser than in female.

Legs. Longer and more slender than those of female. Anterior tibiæ without spurs or apophyses.

Palpi. Femora, patellæ, and tibiæ similar in form, but more slender than those of the female; the hairy covering is longer and more dense, especially on the ventral surface where it is developed into a long thick fringe longest at the distal end. Tarsi short, obliquely cleft, set at an angle to the tibiæ. Palpal organ consists of a subspherical bulb produced on its distal external margin into a slender stem which is curved ventrally and inwardly (Pl. VI. figs. 28 *a* & *b*).

Abdomen. About 1½ times as long as broad; clad with long hair.

Measurements (mm.):—

MALE.

	Length.	Breadth.
Cephalothorax	12·6	10·3
Abdomen	12·8	8·8
Falx	6·5	—

Lengths of	Coxæ.	Tr. & fem.	Pat. & tib.	Met. & tar.	Totals.
Legs I	6·0	16·4	20·0	16·2	58·6
II	5·4	14·3	15·6	14·5	49·8
III	4·4	12·4	12·5	13·8	43·1
IV	5·6	16·6	20·0	19·8	62·0
Palpi	5·8	11·2	14·1	2·7	33·8

Superior Spinnerets; 1·3, 1·6, 2·9 = 5·6.

Localities. Penang, ? alt., 6 ♀ ♀ with egg-cocoons (*Ridley, no date, R.M.*); Penang, ? alt., 1 ♀ with 1 ♂ (? *Ridley, no date,*

R.M.)*; Singapore, 1 ♀ (*Hellier, Jan.* 1900, *R.M.*); Penang, 1500–2500 feet, 1 ♀ (? *coll. May* 1917, *R.M.*); Botanic Gardens, Singapore, 1 ♀ (*Mathieu, July* 1918, *R.M.*) †.

Previous records. "East Indies": the species was described from a single female so labelled ; the above are, therefore, the first definite records of locality for this species.

Specimens. 10 females and 1 male. The male has been deposited in the British Museum (Nat. Hist.) (*ex coll.* Raffles Museum); specimens of the female in F.M.S. Museum, Raffles Museum, and my own collection.

Genus CHILOBRACHYS Karsch.

Chilobrachys Karsch, Berl. ent. Zeits. xxxvi. p. 270 (1892) Pocock, Ann. & Mag. Nat. Hist. (6) xv. p. 171 (1895).

Musagates Pocock, *loc. cit.*

Chilobrachys, id., Faun. Br. Ind., Arach. p. 192 (1902) ; Simon, Hist. Nat. des Ar. ii. p. 956 (1903).

CHILOBRACHYS ANDERSONI (Pocock).

Musagates andersoni (♀) Pocock, Ann. & Mag. Nat. Hist. (6) xv. p. 172 (1895).

Phlogius cervinus (ad. part. ♂), Thorell, Spiders of Burma, p. 5 (1895).

Musagates rufo-fuscus (♀), id., Ann. Mus. Civ. Genova. xxxvii. p. 177 (1897).

Chilobrachys andersoni Pocock, Faun. Br. Ind., Arach. p. 197 (1900).

The collection of the F.M.S. Museum contains a single adult male of this species. The thoracic fovea of this specimen is only slightly procured ; its measurements (mm.) are :—

MALE.

	Length.	Breadth.
Cephalothorax	13·6	11·4
Abdomen	14·5	6·6
Falx	7·5	—

Lengths of	Coxæ.	Tr. & fem.	Pat. & tib.	Met. & tar.	Totals.
Legs I	6·2	17·1	20·0	18·8	62·1
II	5·2	14·7	16·8	16·8	53·5
III	4·4	13·1	13·4	17·1	48·0
IV	5·0	16·6	18·1	22·1 (met.=15·0)	61·8
Palpi	6·0	12·5	15·4	2·4	36·3

Superior Spinnerets : 2·1, 1·7, 4·2 = 8·0.

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* The label of this pair is almost illegible.
† This is the specimen referred to on p. 1117 as being assigned to this species with some doubt.

Locality. Peninsular Siam, no alt. (? *coll.*, *Aug.* 1916, *F.M.S.*).
Previous records. Tenasserim, Mergui, and Karkareet.

Sub-Family DIPLURINÆ.

Group MACROTHELEÆ.

Genus MACROTHELE Auss.

Mygale (ad part.) Walck., Ins. Apt. 1805–37.
Diplura (ad part.) Thorell, Eur. Spid. p. 167 (1870).
Macrothele Ausserer, Verh. z.-b. Ges. Wien, 1871, p. 181.
Diplura (*D. maculata*) Thorell, Rag. Mal. &c. iv. p. 409 (1890).
Macrothele Simon, Hist. Nat. des Ar. i. p. 184 (1892); Pocock,
Faun. Br. Ind., Arach. p. 171 (1900); Simon, *op. cit.* ii. p. 967
(1903).

MACROTHELE FULIGINEA Simon.

Simon, Ann. Soc. Ent. Fr. lx. p. 306 (1891).

A single female exists in the collection of Raffles Museum.
It is apparently very old, is much shrivelled, and has lost its
colour; unfortunately, also, there is no note of the locality where
it was found.

Along with it is a sub-spherical flocculent whitish cocoon,
about 12 mm. in diameter, which contained 112 young spiders.

Previous records. Java; Singapore.

Family ATYPIDÆ.

Genus CALOMMATA Lucas.

Pachyloscelis Lucas, Mag. Zool. cl. viii. p. 14 (1835) *.
Calommata Lucas, Ann. Soc. Ent. Fr. vi. p. 378 (1837).
Pelecodon (*P. sundaicus*) Doleschall, Tweede Bijdr. p. 6 (1859).
Camptotarsus (*C. truculentus*) Thorell, Ann. Mus. Civ. Gen. (2)
v. p. 23 (1887).
Calommata Simon, Hist. Nat. des Ar. i. p. 199 (1892);
Pocock, Faun. Br. Ind., Ar. p. 159 (1900); Simon, *op. cit.* ii.
p. 972 (1903).

CALOMMATA SUNDAICA (Dol.). (Text-figs. 1 & 2, pp. 1121 & 1122.)

Pelecodon sundaicus Doleschall, Tweede Bijdr. p. 6 (1859).
? *Calommata sumatrana* Ausserer, Verh. z.-b. Gesell. Wien,
xxi. p. 130 (1871).
C. sundaica Thorell, Ann. Mus. Civ. Genova, (2) viii. p. 416
(1890) (Stud. Rag. Mal. e Pap. iv.).

Seven small but apparently mature females in my own
collection.

* Wrongly quoted by Simon (Hist. Nat. des Ar. i. p. 199, 1892) and by Ausserer
(*loc. cit. supra*) as "classe VII."

Van Hasselt ("Pelecodon Calommata?"—Tijdschr. Ent. xxviii. p. 89, 1885) shows that the genus *Pelecodon* of Doleschall is identical with *Calommata* of Lucas, and also advances the opinion that *C. sundaica* (Dol.) and *C. sumatrana* Auss. are synonymous with *C. fulvipes* Lucas. Thorell does not find himself able to support this opinion (St. Rag. Mal. e Pap. iv. p. 419), and, from a comparison of my specimens of *C. sundaica* (Dol.)—which agree in every respect with Thorell's long description—with the specimens of *C. fulvipes* Lucas (including the

Text-figure 1.

HC A del.

Calommata fulvipes Lucas.
Right mandible; dentition diagram.

H.C.A. del

Calommata sundaica Dol.
Right mandible; dentition diagram.
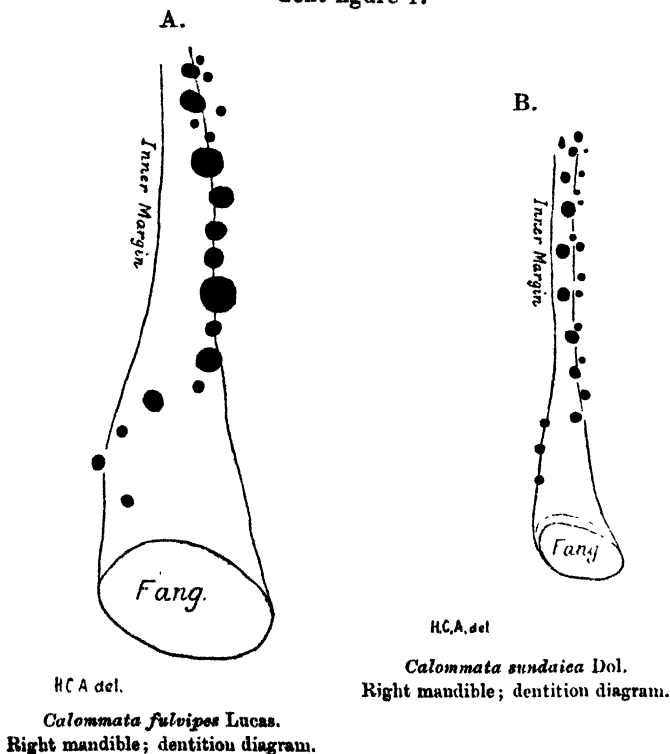
type) in the British Museum (Nat. Hist.) collection, it would seem that the two species are distinct though very closely allied. One easily recognizable difference is the arrangement of the dentition of the fang-groove of the mandibles: in *C. sundaica* this consists of 3 or 4 teeth on the inner margin at the apical end, then a distinct break and the remainder of the teeth follow the outer margin of the groove to its base; in *C. fulvipes*, the teeth at the apical end are on the inner margin of the groove, but the series is continued, without any perceptible break, *across* the groove to the outer margin, and so, along the latter, to its base. (Text-fig. 1, A.)

Measurements (mm.).   Those of the largest specimen are :—

	Length.	Breadth.
Cephalothorax	5·4	4·0
Abdomen	(6·5	?) *
		Depth
Falx	3·3	3·2
Fang	4·1	—

Lengths of	Coxæ.	Tr. & fem.	Pat. & tib.	Met. & tar.	Totals.
Legs I	1·6	3·3	2·4	2·4	9·6
II	1·6	3·1	2·5	2·8	10·0
III	2·2	3·5	2·6	2·1	10·4
IV	2·5	3·5	3·1	2·3	11·4
Palpi.	1·5	3·0	2·2	1·3	8·0

Habits. All the specimens were obtained from a single colony—the only one found,—the members of which had excavated their burrows amongst the roots of a shade tree in hard soil at the roadside.   The burrows were vertically in the ground, with a sill projecting from 1 to 2 mm. above the surface, the entrance being

Text-figure 2.
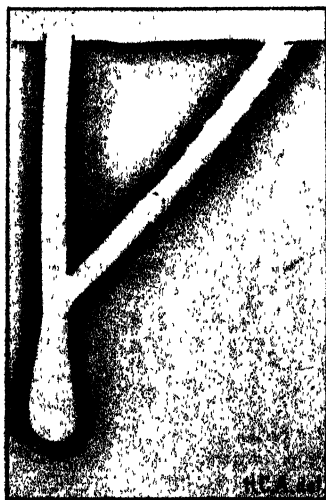
Calommata sundaica Dol.   Diagram of branched burrow.

without any trap-door, but usually concealed by fallen leaves and closed by a sheet of silk; they were lined throughout with very elastic closely-woven silk, which was quite thick, especially near the bottom, where it resembled cotton-wool.   The burrows were

* Abdomen damaged.

usually 60 to 70 mm. long and about 6 mm. in diameter, expanding slightly at the lower end. One example had an upwardly trending branch and appeared to have a valve at the junction, but this is by no means certain, as the lining of the tube was very thick and woolly at that point; it was uncertain whether the branch reached the surface of the ground or not; the general arrangement is shown in the diagram (text-fig. 2, p. 1122). Small stones, rootlets, etc., were found to be frequently woven into the tube linings.

The spiders were exceedingly sluggish and were invariably found at the extreme bottom of their tubes.

Locality. Kranji, Singapore Island (*H. C. A., Jan.* 1923, *A.*).

Previous records. Java and Sumatra.

Specimens. 7 females; these have been divided between the British Museum (Nat. Hist.), F.M.S. Museum, Raffles Museum, and my own collection.

EXPLANATION OF THE PLATES.

PLATE I.

Fig. 1. *Damarchus workmanii* Thorell. Eyes of male.
2.   „   „   „   Right tibia I of male, from inner side.
3.   „   „   „   Left male palp: *a*, from under side; *b*, from inner side.
4.   „   „   „   Diagrams of burrows: *a*, typical branched burrow; *b*, burrow with " back " entrance.

PLATE II.

Fig. 5. *Damarchus cavernicolus*, sp. n. Eyes of female.
6.   „   „   „   Right mandible: *a*, from inner side; *b*, dentition diagram.
7.   „   „   „   Diagram of burrow.
8. *Idioctis littoralis*, sp. n. Eyes of female.
9.   „   „   „   Mandible: *a*, from inner side (left), *b*, dentition diagram (right).

PLATE III.

Fig. 10. *Sipalolasma ophiriensis*, sp. n. Eyes of female.
11.   „   „   „   Labium and bases of maxillæ of female.
12.   „   „   „   Left tibia I of male, from inner side.
13.   „   „   „   Left male palp: *a*, from below; *b*, from inner side.

PLATE IV.

Fig. 14. *Sipalolasma ædificatrix*, sp. n. Eyes of female.
15.   „   „   „   Labium and bases of maxillæ of female.
16.   „   „   „   Left tibia I of male, from inner side.
17.   „   „   „   Right male palp: *a*, from below; *b*, from inner side.
18.   „   „   „   Nest: *a*, view *in situ*; *b*, section along AB.

PLATE V.

Fig. 19. *Lampropelma violaceopedes*, sp. n. Eyes of female.
  20.   „   „   „   Right mandible of female: *a*, from outer side; *b*, from inner side.
  21.   „   „   „   Stridulating spine (much magnified).
  22.   „   „   „   Coxa of palp of female, inner surface.
  23.   „   „   „   Right tibia I of male, from under side.
  24.   „   „   „   Left male palp: *a*, from underside; *b*, from outer side (see note, p. 1111).

PLATE VI.

Fig. 25. *Selenocosmia tahanensis*, sp. n. Eyes of male.
  26.   „   „   „   Left male palp: *a*, from below; *b*, from outer side.
  27. *Coremiocnemis validus* Pocock. Eyes of male.
  28.   „   „   „   Left male palp: *a*, from under side; *b*, from outer side.

ALBINO NAIA TRIPUDIANS

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CYCLAGRAS GIGAS WITH NECK INFLATED.

1-3. OXYBELIS ARGENTEUS.   4, HYLA BLANDSUTTONI, Sp.n.

50. Unrecorded Characters seen in Living Snakes, and Description of a new Tree-Frog.   By JOAN B. PROCTER, F.Z.S., F.L.S., Curator of Reptiles.

(Plates I.–III.)

CONTENTS.

The advantage of studying living specimens, even from the point of view of systematic zoology, is that such a large number of distinctive and enlightening characters of species and genera entirely disappear in spirit-specimens, and are consequently ignored in diagnosis.   Also from bleached and very often rigidly-set pickled specimens, one learns nothing of the species in nature. Since I had the advantage of working under this Society it has been impressed upon my mind that Museum work, however accurate, requires confirmation and a great deal of elucidation from field-notes and the study of the living things.   We should learn so much more if collectors would make notes of the characters lost in death, rather than in preserving such large numbers of individuals –a method which is being put into force by most of the recent American Zoological expeditions.

I. *An Albino* Naia tripudians.   (Plate I.)

Albino Snakes are excessively rare, and, although individuals of various species have been recorded from time to time, I cannot find any reference to an albino Cobra. The specimen which has been living in the Reptile House since the end of August is, further, unique in being fully grown and active, with bright eyes and the bloom of health upon its scales.   With the exception of a thin powdering of very light brown pigment on the back of the hood, this Cobra is colourless; ivory above and pure white beneath, the skin between the scales is transparent flesh-pink, and tiny red blood-vessels can be traced on the lips.   The tongue and entire inside of the mouth are also pale flesh-pink, and the eyes are ruby-red.   The tinge of brown on the hood merely adds to the general wraith-like effect by faintly outlining the characteristic " spectacles," which marking is in itself curiously asymmetrical, as can be seen on Plate I.

This Snake is the property of Mr. J. C. Roberts of Delhi, who caught it himself and keeps it as a pet.   He has lent it to the

Society at the request of Lord Reading. who was much struck with it. The loan is especially kind, as Mr. Roberts not only places a very high value on it as a specimen, but is also very attached to it, carrying it about everywhere with him, and allowing it to caress him. It was therefore a wrench for him to leave it in the Reptile House on his return to India, for Cobras are very delicate, and frequently pine away in captivity. So far, however, it is feeding well, and whilst it is in such splendid condition we have been fortunate in securing a cinematograph film and several good photographs of it at close range. A copy of the film taken by the British Instructional Film Company is being deposited in the Society's library.

II. *The Hood of* Cyclagras gigas *and other examples of neck inflation.*

In 1921 Dr. Kingsley Noble, of the American Museum, New York, published an interesting paper on " Snakes that Inflate," in which he reviewed the various manners in which Snakes inflate or dilate their necks. He found that many of the species which inflate their necks, like the South African Boomslang, do so by means of a tracheal lung or diverticulum. *Dispholidus typus, Dipsadomorphus trigonotus, Thelonortus kirtlandii,* and *Spilotes pullatus* do this. He also gives *Coluber radiatus* as an example. A specimen of this Rayed Snake from Hong Kong, recently living in the Reptile House, used to improve on the more usual type of " frightfulness " by compressing its neck vertically in the opposite direction to a Cobra's hood, the neck being at least three times its proper width in profile, and knife-edged when viewed from above. At the same time the Snake assumed a " striking " attitude, hissing loudly. The hissing, or exhaling of the air from the trachea after the primary inflation, probably produces this hatchet kind of hood, which has apparently not been observed before.

Another case of neck-dilatation is that of *Cyclagras gigas*, an exceedingly fine Water-Snake allied to *Xenodon*, a genus which is known to flatten the neck when alarmed. Three specimens of *Cyclagras* at present living in the Reptile House go much further than this, spreading a hood quite as large as that of a Hamadryad upon the very slightest provocation. This hood is shaped like the Cobra kind, and does not at all resemble the sort of flattening seen, for instance, in the case of the Hog-nosed Snakes (*Heterodon*). On dissection one finds that the cervical ribs are quite as long, if not a little longer than those of the rest of the body, and that they are folded to the sides longitudinally when the Snake is in repose and the neck itself comparatively slender. This condition is also met with in the Hamadryad, *Naia bungarus* : so *Cyclagras* evidently spreads its hood in the true Cobra manner by the lateral elevation of the ribs. In *Naia tripudians* the ribs are, of course, very much

more developed. It is an odd coincidence that, although living in South America where there are no Cobras, this Water-Snake resembles the Hamadryad in form, size, shape of head, colour, markings, hood, and " striking " mode of attack—so much so, that, on the first occasion when it attacked me in this way, I thought for a moment that I had got hold of the Hamadryad by mistake. If the two genera inhabited one continent they would certainly be cited as a case of mimicry, instead of yet another instance of the parallel development so continually met with amongst Reptiles and Batrachians*.

III. *The Tongue of* Oxybelis argenteus *Daud.*

It is generally supposed that the tongues of Snakes are black or dark grey, and it was therefore a surprise to find that the tongue of the Silvery Tree-Snake is coloured and marked to match the rest of the head. The upper surface is olive green-grey even to the slender bifid tips; the sides continue the dark streak which is present throughout the length of the body from the tip of the snout. The lower surface is cream-coloured like the throat, with a continuation of the tiny black dots which are present on the chin. Now as the tongue is as broad as the tip of the extremely acuminate snout, it appears to be a continuation of it when hovering in and out, especially when the tongue is protruded through the rostral nick with the lips closed. The effect of " pulling faces " is really most arresting to witness, and is utilized by the Snake to fascinate the Lizards upon which it preys. I have seen it doing this, the Lizard watching the hovering tongue in perplexity, quite engrossed, and the Snake striking at close range without startling the usually swift and cautious prey.

The tongues of spirit-specimens are usually retracted into the basal sheath and rigidly set. It is, however, possible to dissect them out, and I find that all three species of *Oxybelis* share this peculiarity of harmoniously coloured tongues. More recently the Society received the Indian Tree Snakes *Dryophis mycterizans* and *Chrysopelea ornata*. The former has a light greenish tongue, yellowish beneath, and the latter has a scarlet tongue irregularly spotted with black and matching the general coloration very well.

IV. *Description of a new Species of* Hyla.

Amongst a small collection of live Reptiles and Batrachians from Australia, recently purchased by the Society, is a beautiful Tree-Frog of the genus *Hyla*, which belongs to a new species, which I propose to call *blandsuttoni* in honour of Sir John Bland-Sutton.

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* Since writing the above, Major Flower informs me that this resemblance to the Hamadryad has actually been given as a case of mimicry, but we have not been able to locate the reference.

HYLA BLANDSUTTONI, sp. n.

Description.

Habit raniform. Head longer than broad; snout obtusely pointed, canthus rostralis distinct, loreal region very oblique, somewhat concave; nostril twice as far from eye as from tip of snout; interorbital space as wide as or a little narrower than the upper eyelid; tympanum distinct, oval, about $\frac{3}{4}$ the diameter of the eye.

Fingers free, first slightly longer than second, and used as a thumb in life *; toes $\frac{3}{4}$-webbed, leaving two phalanges of fourth toe free; digital discs small, as in *H. arborea,* those of fingers and toes equal; subarticular tubercles moderately developed, a small oval inner metatarsal tubercle and a slight tarsal fold. Tibia $4\frac{1}{2}$ times as long as broad; tibio-tarsal articulation reaching the anterior corner of the eye when the hind limb is adpressed.

Skin finely granular above, coarsely so beneath, the parts of the legs which are usually concealed are, however, covered with very delicate smooth skin; a dorso-lateral glandular fold extending from the posterior corner of the eye almost to the groin; a second, indistinct and broken up on each side of the back.

Coloration: iridescent bronze on all exposed upper surfaces, with a dark canthal streak which continues on the temporal region; throat white; abdomen and lower surfaces of thighs bronzy. All parts which are hidden when the Frog is at rest (*i. e.,* axillæ, flanks, groins, and "flash" portions of legs and feet) brilliant torquoise-blue, shading to sapphire in the axillæ and groins. Iris metallic copper. The striking "flash" colours are, of course, only exhibited when the Frog is jumping or climbing, and will no doubt fade after death. In repose the general bronze effect is entirely inconspicuous.

Affinities.

Allied to *H. aurea,* from which it differs in the following particulars:—

H. aurea.	*H. blandsuttoni.*
Canthus rostralis :	
rounded.	sharply marked.
Nostril :	
equidistant from eye and end of snout.	about twice as far from eye as from end of snout.
Fingers :	
moderate in length, first equal to second.	long, first longer than second.
Toes :	
entirely webbed, one phalanx of fourth free.	$\frac{3}{4}$-webbed, two phalanges of fourth free.
Discs :	
hardly developed, no wider than penultimate phalanges of digits.	small but wider than penultimate phalanges, shaped as in *H. arborea,* not as in *H. rubella.*
Habit :	slenderer in build than *H. aurea.*

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* *Hyla aurea* also uses its 1st finger as an opposable thumb.

Habitat. Queensland. This must, however, be regarded as uncertain, because the Frog was purchased, and the person from whom it was bought touched at a good many Australian ports, and as he did not leave an address it is not possible to verify the type-locality.

Type. The type-specimen is an adult female, at present living in the Reptile House. After death it will be presented to the British Museum (Natural History). A coloured plate of it is given, since when it is dead the whole of its characteristic and very beautiful " flash " colours will disappear.

EXPLANATION OF THE PLATES.

PLATES I.-III.

I. Photo of albino *Naia tripudians*.

II. Photo of *Cyclagras gigas* with neck inflated.

III. Colour-drawings of head and tongue of *Oxybelis argenteus*, and of *Hyla blandsuttoni* in a climbing attitude.

51. On the Anatomy and Systematic Position of the Mada-
gascan Bird *Mesites* * (*Mesœnas*), with a Preliminary
Note on the Osteology of *Monias*. By PERCY R. LOWE,
B.A., M.B., F.Z.S.

[Received October 21, 1924; Read November 18, 1924.]

(Text-figures 1–7.)

Isidore Geoffroy Saint-Hilaire (13) in the year 1838 was the
first to make known to the scientific world the existence of this
peculiar Madagascan bird, which is flightless. It was a mixture
of so many characters recalling, to his mind, so many bird-groups
that he placed it in a new genus, *Mesites*.

Milne-Edwards † has given a review of the many attempts
to arrive at a satisfactory conclusion as to its systematic position.
It had been placed among the Megapodes and even among the
Passeres, while between these widely separated groups a goodly
array of families, and even orders, bears testimony to the treat-
ment it has met with at the hands of eminent ornithologists
of past days. For an appreciation of this and for the sake of
economy in space, the reader must be referred to the literature
appended.

In 1876, or early in 1877, the Zoological Society of London
received two skins among a consignment of birds from Mada-
gascar, and Bartlett (1), with an intuition almost amounting to
genius, arrived at the conclusion, as the result of a study of these
dried husks, that *Mesites* should be placed near to *Eurypyga* and
Rhinochetus (the Sun-Bittern and Kagu). About the same date
two specimens, " in the flesh," preserved in alcohol, arrived in
Europe. These went to Paris, and Milne-Edwards (*l. c.*), as a
result of his dissections, concluded that " elles doivent prendre
place dans le groupe des Echassiers où elles forment une famille
bien caractérisée voisine de celle des Râles et de celle des
Hérons."

Forbes (5), who wrote a paper in 1882 upon the feather-tracts,
came to the conclusion that " *Mesites*, *Eurypyga*, and *Rhino-
chetus* have all sprung from some common ancestor. which must
have been a generalised Pluvialine form provided with powder-

down tracts." But it must be noted that most probably the only material Forbes had was two skins.

Since then, so far as I am aware, no one has had anything to say about this ancient and generalised bird; nor do I think that, since Milne-Edwards received his specimens forty-eight years ago, any more examples suitable for anatomical study have arrived in Europe, until in the early part of 1924 the British Museum were able to acquire some. As a result of my examination of these, I hope that there may be some justification for the following notes, which are offered in either amplification of, or addition to, the sum total of our knowledge of a bird which from the nature of its anatomical features ought to shed some little light upon the evolution of the Gruiformes and their relation to neighbouring avian stems. I may add, as an additional excuse for this paper, that Milne-Edwards was unable to examine the intestinal tract of *Mesites*, while the figures which he gives of the feather-tracts are so at variance with the results obtained by me that I am led to conclude either that he was very badly served by his artist or that the specimens which he received were in such a bad state of preservation that accurate study of the pterylosis was impossible (but see under *Mesites unicolor*). Moreover, the figures given of the skull are so crude as to be nearly useless for conclusions of any value to be drawn from them. Finally, I might add that Gadow [*] places *Mesites* in his Galliformes along with the Turnices, Galli, and *Opisthocomus*. I mention it here, as I am convinced that there is really no sound reason to believe that *Mesites* contains any characters which one could say were purely gallinaceous, therefore I shall not further consider its possible Galline relationships.

I have already given some reasons ('Ibis,' 1923, p. 293) which would seem to justify the complete removal of the Turnicomorphs from the Galli.

One of the minor points of interest about *Mesites* is its legs and feet in respect of the character of the epithelial scales forming the podotheca. This has been already noted by the older writers. The only remark therefore which I shall make here is to call attention to the fact that the feet of *Mesites* are obviously adapted to an arboreal life. This is remarkable in a bird which has been described by Milne-Edwards as not only flightless but a runner. Curiously enough, Geoffroy St.-Hilaire has referred *Mesites* to the Pigeons, this being suggested on purely superficial characters. The morphology of its lacrymals and ectethmoids, the quadrate and its tympanic relations, as well as the pelvis, might possibly be interpreted as reflecting Columbine factors, but it is more likely that they only point to a very generalised avian type.

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[*] Bronn's Thier-reich, Vögel, ii. p. 165.

Mesites unicolor.

In 1845 Des Murs (4), in the ' Revue Zoologique,' on page 176, described under the above name what he considered to be a new species of the genus *Mesites*. Milne-Edwards in 1879, in the ' Histoire Naturelle de Madagascar,' considers this to be merely the female of *M. variegata*, the species originally described by Geoffroy St.-Hilaire *. A consignment in spirit, lately imported into this country from Madagascar, consists of nothing but the uniformly-coloured bird—the so-called *Mesites unicolor*; and Lord Rothschild informs me that the same applies to birds which he has lately received at Tring. One of the specimens in the flesh recently purchased by the British Museum is undoubtedly a male, as proved by microscopic examination after sections had been cut. There is therefore ground for the inference that there may be two species of *Mesites* after all, although it may be possible, though I do not think very probable, that the bird just referred to may be a young male in the early female phase of plumage. In any case, it seems highly improbable that, in a consignment consisting of ten or twelve specimens in all, there should not be a single male.

If there really are two species, it may possibly explain the conspicuous difference between the figure depicting the powder-down and other tracts given by Milne-Edwards and that given by me in this paper.

It should therefore, I think, be borne in mind that the following notes may refer to another species than that described by Milne-Edwards.

Bill.—The nostrils of *Mesites* occupy the middle third of the maxilla, and are overhung in their entire length by a soft membranous or horny operculum whose lower edge is somewhat inturned, slightly convex, and parallel with the dentary margin of the premaxilla. As a result, the nasal opening presents itself as a mere slit directed downwards and slightly outwards. Forward of the nasal opening there is no indication of a nasal groove, while posterad of the slit the soft opercular covering is continued backwards to the frontal feathering. In *Rhinochetus* there is a deeply sculptured nasal depression, in the middle of which a much incurved, prominent, and isolated nasal operculum overhangs the nasal orifice, so that this latter lies at the bottom of a deep groove.

In *Rhinochetus, Eurypyga,* and the Rails, in contradistinction to *Mesites*, a deep and elongated groove lies anterad of the nasal orifice ; but, although resembling to a slight extent the condition to be seen in *Rhinochetus* (a much specialised one), the external nasal opening in *Mesites* is like none of these, nor is it columbine, but seems to resemble the arrangement to be observed in *Turnix*, although by this we are far from suggesting anything in the way of affinity, except that both are generalised and ancient types.

* Compt. rendus Ac. des Sci. t. vi. 1838, p. 443.

VISCERAL ANATOMY.

Alimentary Canal.—On opening the bill, the *hard palate* presents three parallel and longitudinally disposed rows of papillæ—one central and two lateral. These papillæ have the appearance of backwardly directed spinous processes. The same spiny protuberances arm the edges of the tongue and soft palate (*cf.* text-fig. 1). Distad of the three palatal spinous rows are three protuberances which resemble small pads, which are probably used for holding insects, etc.

Of a *crop* I could find no indication.

Stomach.—The proventriculus is nearly an inch long, and appears to be uniformly lined throughout its whole extent with a well-marked glandular and foveated epithelium. It is sharply

Text-figure 1.
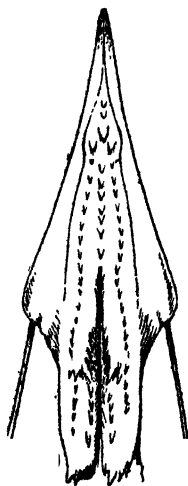
Soft palate of *Mesites.*

constricted from the gizzard, which is very muscular (muscle-wall equalling 10 mm. in thickness), hard, and lenticular in shape. The gizzard is lined with a very tough corneous coat, easily separable from the epithelial wall, and forming a distinct sac. The inner surface is thrown into well-marked longitudinally-disposed rugæ.

Intestinal coils.—If my interpretation is correct, the intestinal tract of *Mesites* resolves itself into three simple and primitive loops, of which only the mid-coil of Meckel's tract presents a secondary loop, which latter, however, may represent the fourth loop. The duodenal and supra-duodenal loops appear to be quite simple. Although I made a careful and prolonged search I could find no trace of a Meckel's diverticulum in any part

of Meckel's tract. The most interesting and conspicuous feature of the intestinal tract is, however, the large size of the cæca and their distal extremities. These cæca arise on either side of the proximal end of a somewhat dilated and nearly straight rectum, 29 mm. in length. For the first inch or so from this origin they are somewhat simple, narrowed and thick-walled tubes, becoming more dilated and somewhat sacculated in their course forwards to their distal extremity, where they are suddenly constricted to two narrow thick-walled tubes, sharply bent on themselves (see text-fig. 2), and suggestive of "vermi-

Text-figure 2.
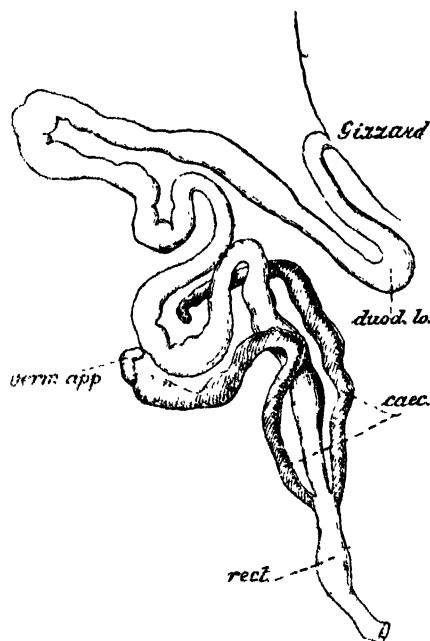
Drawing of Intestinal Tract of *Mesites*.

cæc., cæca; *verm.app.*, "vermiform appendices" of cæca; *rect.*, rectum;
duod.lo., duodenal loop.

form appendices." The cæca have a length of 55 mm. or rather more, and contained food-stuff in a semi-digested but not fluid state. The "vermiform processes" have a length of about 13 mm. or more, and one of them (the left) was attached to the mesentery within the supra-duodenal loop. So far as I am aware, these appendices are absolutely unique in the avian class. As regards those portions of the cæca which contained food in obvious process of digestion, the walls were thin and the lumen wide, presenting nearly the same appearance and width as the rest of the intestine.

Neither Milne-Edwards nor Chalmers Mitchell, in his classical treatise on the bird's intestinal tract, were able to procure material to describe the peculiar condition indicated above.

Excluding the extraordinary "vermiform appendices," the general disposition of the intestinal convolutions of *Mesites* appear to be rather more reminiscent of those of *Rhynchea capensis*, described and figured by Chalmers Mitchell [*] than of any other form I have been able to compare them with; but they also somewhat closely resemble those of the Cariama [†]. Whatever the case may be, the arrangement seems to answer to the type of gut which Chalmers Mitchell (10) would, I believe, term archecentric or primitive. At any rate, the condition seems one that we might have expected to find in a bird which is evidently one of great antiquity and generalised.

Text-figure 3.
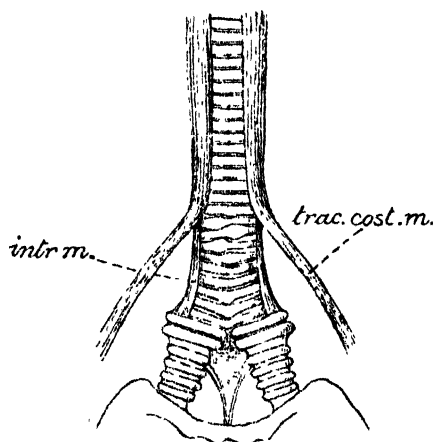
Syrinx of *Mesites.*

intr.m., intrinsic muscles; *trac.cost.m.*, tracheo-costal muscle.

The Syrinx.—*Mesites* seems to present us with a primitive and somewhat simple syrinx of the tracheo-bronchial type. It is furnished with a pair of extrinsic and a pair of intrinsic muscles. The extrinsic, in the complete absence of a clavicle, have an attachment which is situated further back than is usual, viz. on the first sternal rib. The intrinsic do not extend further than the first bronchial ring (*cf.* text-fig. 3). The first two bronchial rings are slightly specialised, and so are the last three tracheal. The 6th, 7th, and 8th tracheal rings are somewhat expanded and protuberant on their anterior aspect.

The *trachea* is quite simple and exhibits no tendency of any kind to specialization.

Viscera.—I found two carotids in the specimen I dissected.

* P. Z. S. 1905, p. 157.   † Beddard, ' Classification of Birds,' p. 323.

Pterylosis.

Oil-gland.—Forbes (5), from an imperfect specimen, was unable to be sure if the oil-gland was tufted or not. Milne-Edwards (*l. c.*) does not refer to the question. In the specimens (in the flesh) which I have examined there is not the faintest indication of the presence of an oil-gland at all, although I searched diligently with a strong glass. The oil-gland, it may be noted, is absent in the Bustards and *Struthio* and may also be wanting in the Pigeons.

Confirmatory of Forbes's findings I could discover no aftershaft to the contour-feathers, although an aftershaft is present in *Grus* and the Rails. It is, however, absent in *Heliornis* and *Podica*, both of which are undoubtedly Rails.

Pteryla alaris.—There does not appear to be even a rudiment of a claw on the pollex. The ala spuria (pre-primaries) is remarkable for its large size, its feathers extending beyond the primary coverts (about half an inch) and nearly halfway down the outer primary wing-feather.

Carpal remex and covert.—Contrary to what I think is the usual disposition, I found that in both *Mesites* and *Parra jacana* [*] these feathers belonged to the primary series (not the secondary), the covert being disposed on the distal side of the remex and the remex in a direct line with the first primary covert. This was especially obvious in *Parra*, in which the covert was distinctly larger than the remex.

The wing is quinto-cubital (eutaxic), wherein it differs from the Cranes [†], Rails, Plovers, Jaçanás, and Herons. On the other hand, the wings of *Heliornis* and *Podica* agree with *Mesites* in being eutaxic.

There are ten primaries, of which either the third or fourth appear to be the longest (first primary counted as the innermost). The wing is short and rounded, and from the longest primary the feathers decrease in uniform sequence distally.

Pteryla caudalis.—A very noticeable feature of *Mesites* is its long and strongly-developed tail, in which there are sixteen rectrices. Equally remarkable are the fourteen upper and fourteen lower tail-coverts, which are nearly as strong as the rectrices proper and attain to three-quarters their length or more. In one specimen they were nearly as long as the rectrices.

For purposes of comparison with what obtains in the Rails, I may add that they measured in one specimen 115 mm., the body of the bird in question measured from the root of the tail to the sternal notch, being only 80 mm.

Pteryla femoralis.—This is a remarkably well-developed tract, as we have endeavoured to indicate in the text-figure 4, while in front of it three or four rows of quite strong feathers in parallel

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[*] I am in agreement with Milne-Edwards in regarding the Parridæ as Rails and not Plovers.

[†] The Cranes may be eutaxic.

and orderly sequence are to be noticed. Whether one is justified or not in the thought, these last seem to be suggestive of coverts; while the feathers of the actual femoral tract seem strong and long enough to suggest the relics of primitive crural remiges *. Indeed, the long tail with its remarkably well-developed rectrices and coverts, the strong femoral tract (suggestive of a supernumerary flying factor) combined with the long cursorial and muscular legs, and the reduced wings (correlated with even more remarkably well-developed pectoral muscles) seem to be

Text-figure 4.

A   B
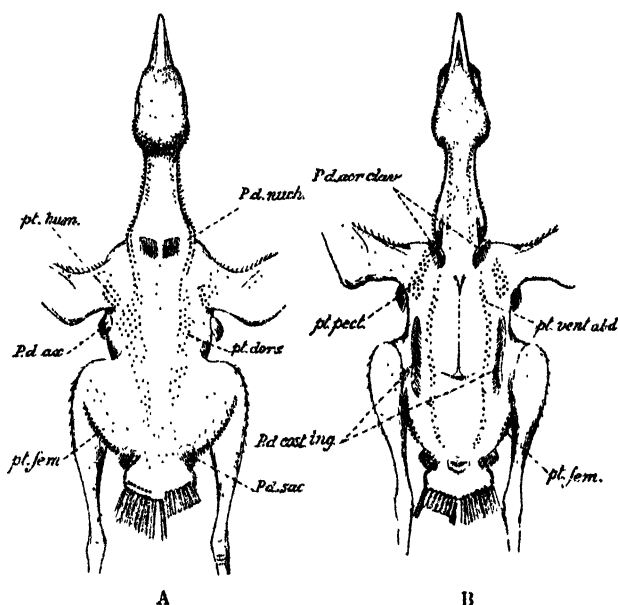
Drawing of the Feather-tracts of *Mesites*.

A. Dorsal aspect. B. Ventral aspect.—*pt hum.*, humeral tract; *pt dors.*, dorsal tract; *pt.fem.*, femoral tract; *pt.pect.*, pectoral tract; *pt.vent abd.*, pteryla ventralis abdominalis; *P.d.nuch.*, nuchal powder-down patch; *P.d.ax.*, axillary powder-down patch; *P.d.sac.*, sacral powder-down patch; *P.d.acr.clav.*, acromio-clavicular powder-down patch; *P.d.cost.ing.*, costo-inguinal.

a valid excuse for conjuring up a picture of a primitive bird whose ancestors ran along the ground like one of Baron Nopcsa's Preo-Aves †.

Pteryla capitis.—This is very nearly continuous, except that there is a very definite circumorbital bare space and an indication of a supra-orbital one situated above and to the inner side of a strong supra-orbital tract. There is no circum-aural apterion such as is found in the Herons and Bitterns.

* See Beebe, Zoologica, vol. ii. No. 2—"On the Pelvic Wing."
† Cf. P. Z. S. 1907, p. 285.

As regards the remainder of the feather-tracts, their form and disposition give a distinctly ardeine impression, and in this respect, especially when considered in conjunction with the five pairs of powder-down patches present in *Mesites*, I have seen nothing so much like that which obtains in this form as the feather-tracts of *Cancroma* (Boat-bill), *cf.* Nitzsch's 'Pterylography,' pl. viii. figs. 13 and 14.

Milne-Edwards (9) figured the powder-down patches of *Mesites*, but the figure is not only very crude but, unless *Mesites variegata* is an entirely distinct species from *Mesites unicolor*, it bears little or no resemblance to the actual condition of things. Moreover, it does not include the actual feather-tracts. Forbes (*l. c.*), however, describes these (from skins) but gives no figure. The drawing now produced is, I think, justified, as I believe it represents the actual facts in an especially accurate way and reflects in no small degree Mr. Grönwold's habitually careful work as an artist.

Bartlett (1) first described the powder-down patches, and suggested that the genus *Mesites* should be "arranged in the Natural System next to *Eurypyga* and its near ally *Rhinochetus*."

It might be as well, in order to facilitate comparison with other patches in other forms, to name these as follows :—

(1) *The nuchal pair*, situated on the back of the neck on either side of the middle line in the long dorsal apterion.

(2) *An axillary pair* whose name denotes its position.

(3) *A sacral pair* situated on either side of the base of the uropygium.

(4) *An acromio-clavicular pair* seated on either side over the site of the acromial head of the scapular and extending downwards and inwards for some three-quarters of an inch, along what would have been the line of the furculum had it existed.

(5) *A costo-inguinal pair* situated outside the *pteryla ventralis abdominalis*.

The nuchal and acromial patches appear to have so upset the ordinary normal arrangement of the dorsal and ventral tracts that it is a little difficult at first to follow them in their altered position. It seems clear, however, that the *Pteryla colli* extends downwards from the chin, malar, and aural regions as a continuous and moderately strong tract (feathers reddish) almost as far as the middle of the neck. Here it splits into two strong and conspicuous tracts, situated on the ridges of two folds of skin, which are continued backwards on either side of the front of the neck to nearly as far as the sternal notch and end interad of the inner extremities of the acromial powder-down patches (*cf.* text-fig. 4, B). The acromial patches have so interposed themselves that the *Pteryla ventralis pectoralis* have become not only to a certain extent displaced from their usual position, but they are completely cut off and isolated. They have also cut off the *Pteryla ventralis abdominalis* from continuity with the *Pteryla*

colli, a continuity which is normal in a Ralline or a Charadriiform bird. Indeed, the disposition of this isolated tract (*P. ventralis abdominalis*) seems not altogether unlike the condition seen in a quail or a turnicomorph (*cf.* 'Ibis,' 1923, p. 281).

Turning to the dorsal region, we find a most peculiar arrangement of the tracts (*cf.* text-fig. 4, A), the main thing to be noted being the very long and wide central apterion which extends from the occiput to well down upon the sacrum, and is only interrupted by the nuchal powder-down patch and a few degenerate feathers (not down) posterad of these, the interpretation of which last I am unable to supply.

Except in the Herons I know of no similar instance of the *Pteryla colli dorsalis* forking in this manner from its very commencement, so that the central apterion extends the complete length of the neck from the occiput. It is to be noted that the *lateral neck-space* between the ventral and dorsal cervical pterylœ would seem at first sight to only extend halfway up the neck, but I have not satisfied myself that there is not, at least, a potential bare space which continues forwards almost to the aural region; at any rate, the ventral and dorsal cervical pterylœ appear to be quite distinct from one another in their complete extent, the line of separation being marked by this potential apterion.

Forbes (*loc. cit.* p. 271) sums up his paper on the pterylosis of *Mesites* thus:—"I should be inclined therefore to consider that *Mesites*, *Eurypyga*, and *Rhinochetus* have all sprung from some common ancestor which must have been a generalised Pluvialine form provided with powder-down tracts." If by Pluvialine he meant to indicate a strictly Charadriiform type I can see little justification for the inference, and as I have indicated above I should be inclined to regard the facts as pointing to a generalised Ardeine or Gruiform ancestor.

Myology.

Under this heading I have only a few observations to make, the time at my disposal for prolonged dissections having been unfortunately wanting.

As regards the fore-limb the strong development of the sterno-humeral muscles is at once evident, and in a bird described as flightless is somewhat surprising. The *pectoralis major* is distinctly over than under developed. It takes origin from the largest amount of sternal surface possible, some fibres slightly overflowing on to the abdominal aponeuroses. There seems to be a distinct tendency to a division into two parts, an upper and outer and an inner and lower, which in their insertion still maintain their identity. Since in *Mesites* the clavicle is entirely absent, the muscle derives no origin from that bone nor does it seem to get any support from the coraco-sternal ligament.

The *pectoralis secundus* is also a very well-developed muscle ; its fibres in passing upwards and outwards to its insertion

converge to a thin and glistening tendinous surface which lies on the upper surface of the muscle, and finally winds round the inner side of the coracoid as a rounded tendinous cord to reach its insertion on the humerus. There is, of course, no foramen triosseum. The coraco-sternal aponeurosis or ligament seems merged into the inner border of the muscle.

The *pectoralis tertius* presents nothing abnormal.

The *deltoid* is a well-developed muscle. The brevis portion comes well down beyond the middle portion of the humerus, and the longus and brevis are merged above into one.

The *biceps* is a degenerate muscle in *Mesites*. The short head is only vaguely to be made out and the long head not very well developed. I made out a biceps slip, however.

The *triceps* is a finely developed muscle: two heads could be made out, the humeral and scapular. It is a very much bigger muscle than in the Common Rail.

The *patagial muscles* and tendons were not easy to dissect—firstly, on account of their poor development, and, secondly, on account of the very friable state of the muscle-fibres due to some fault in preservation.

Not to waste space, it may be shortly said that all the muscles of the forearm seemed as well developed and as normal as in any ordinary bird capable of flight of the same size as *Mesites*.

Hind limb.— All the muscles of the thigh and leg were hyper-developed. I exposed a semi-tendinosus, an accessory semi-tendinosus, a femoro-caudal, an accessory femoro-caudal, and an ambiens.

The tendon of the last muscle just before and after piercing the aponeurotic covering of the knee-joint became much attenuated, and I was unable to trace if it had any actual connection with the *flexor perforatus,* but it seemed to me to be lost on gaining the knee-joints.

Osteology.

Vertebral Column.—*Mesites* has 15 cervical vertebrae, 2 cervico-dorsal (furnished with floating ribs), and 5 dorsal (furnished with ribs which reach the sternum).

In *Rallus aquaticus* there are 13 cervical, 2 cervico-dorsals, and 7 dorsals. In *Grus* the number of cervicals is seventeen.

In *Mesites* the atlas is notched for the odontoid process of the axis, and this condition obtains in the genus *Grus* as well as in the Rails.

In *Mesites* from the 6th cervical posterad to the 11th there is a continuous series of catapophysial processes on the ventral aspect of the centra, which although in pairs are sufficiently far apart as not to suggest the least tendency to approach one another in the formation of a catapophysial canal such as may be seen for example in the Herons. On the 12th cervical there is a sudden transition to a bifid hypapophysis, while on the

13th, 14th, 15th, and 16th the hypapophyses present the form of single laterally-compressed median projections, that of the 13th being rather like a "cap of liberty" seen in profile. In *Grus virgo* there is, allowing for the more numerous cervical vertebræ, a rather impressive similarity to the condition in *Mesites*—for instance, the catapophysial processes start on the 5th cervical and continue backwards to the 15th. On the 16th cervical there is a conspicuous bifid hypapophysis, and then follow two simple ones on the 17th and 18th.

Beddard * has called attention to the same condition (allowing for differences in the number of vertebræ) in *Aramus*, and compares *Aramus* with *Grus carunculata, Balearica, Tetrapteryx,* etc., so that, without going into further details and comparisons, I think we may take the condition just noted in *Mesites* as being a very strong piece of evidence pointing to a gruiform phylogeny, more archicentrically gruiform indeed than the Rails, which I regard as specialised Gruines, just as the Gulls are specialised Charadriines.

Finally, in the vertebral column of *Mesites* I note that the last cervical and first cervico-dorsal vertebræ present two conspicuous and isolated neurapophyses which stand out in sharp contrast to the plain neural arches of the vertebra immediately anterad and posterad of them. The first two dorsal take part in the formation of somewhat conspicuous hypapophyses which are fused into a single mass.

Excluding the pygostyle there are five free caudal vertebræ, upon the last of which I make out a bifid hypocentrum.

Skull.—Base: (1) There is a downwardly projecting median ridge on the ventral surface of the basisphenoidal rostrum which seems to me somewhat ardeine in character. I do not recall having seen such a ridge in any group save the Herons.

(2) The *occipital condyle* presents only the very faintest trace of a bi-lobed condition, which seems to be a ralline character. In Herons, Cranes, Kagu, and Sun-Bittern it is *distinctly* bilobed.

(3) The *foramen magnum* is cordate in shape, a condition which is more or less constant in the Rails. In the Kagu it is nearly circular. In position it is more ralline than charadriine.

(4) There are no supra-occipital foramina, such as are found in the Cranes and Charadriidæ, but not in the Rails, Herons, Kagu, and Sun-Bittern.

(5) To save space, I may shortly state that the following parts about the base or occipital region of the skull in *Mesites* present features which come very close to a ralline or in most points, and perhaps more accurately, to a gruine picture:—The supra-occipital with the lambdoidal ridge and the faintly sculptured temporal fossæ above it; the cerebellar protuberance; the basi-occipital and pre-condylar fossa; the paroccipitals; the basi-temporal plate and mammillary processes; the tympanic fossæ;

and the squamosal, postorbital, and zygomatic processes. Indeed, if one drew a line from one postorbital process to the other it might be said with truth that the morphology of all the parts behind this line was ralline, pure and simple, by which I mean to imply a complex which is rather more specialised than the more archecentric gruine type.

(6) As regards the tympanic fovea there is one character which is particularly ralline, and I draw attention to it here because I have lately discovered it to be so characteristic of the Rails in general, and of great service in differentiating them from neighbouring groups, such as the Charadriiformes. In fact, I have used it (in conjunction with other characters) in a paper now appearing in 'The Ibis' to separate the Parridæ from the latter group and to unite them once more with the Rails, a family to which I have convinced myself they ought to be referred.

The character referred to is the forward position of the quadrato-tympanic articulation combined with the markedly trabeculated and pedicle-like structure on which the inner head of the quadrate rests and with the cutting away of the posterior edging of the tympanic fovea (paroccipital)—all of which tends to produce a very characteristic and easily recognised condition which is constant in all the twelve Ralline genera whose osteology I have examined, as well as in the Gruidæ. Judged by this easily recognised character-complex, *Mesites* is ralline, *Rhinochetus* and *Eurypyga* are more ardeine than ralline, while the Parridæ are undoubtedly ralline (*cf.* 'Ibis,' Jan. 1925). In this character-complex the Gruiformes, including the Rails, seem to be very easily distinguished from the Charadriiformes as defined by me in 'The Ibis' of 1922 (p. 489), while the Galliformes are conspicuously isolated from all, and the Pigeons recede from the Charadriiformes.

(7) In *Mesites* the palatine plates, maxillo-palatines, and vomers are distinctly gruine, the maxillo-palatines being even more gruine than *Grus*, so to speak. In other words, the maxillo-palatines are hidden, when viewed from below, by the pre-palatals, which are narrower than the posterad portion of the plates (*cf.* text-fig. 5). The square-cut ends of *Rhinochetus* and *Eurypyga* are ardeine—their maxillo-palatines gruine.

(8) *Nostrils.* In the Rails, as is well known, a condition of holorhiny obtains, and the same condition is present in the Storks and Herons. In the Cranes, *Rhinochetus*, and *Eurypyga* the condition is schizorhinal; while in *Mesites* it is *neither one nor the other*, but is perhaps more schizorhinal than holorhinal—the condition being as in *Furnarius*, *Cursorius*, etc.

It seems difficult to extract much satisfaction from an evolutionary or taxonomic point of view from a study of the holorhinal or schizorhinal condition; but it may be noted that in a provisional classification of the Charadriiformes which I attempted in 'The Ibis' for July 1922, the true Limicolæ (Charadriidæ and Scolopacidæ), which I regarded as being

archicentric for the group, are schizorhinal; and this condition is correlated with the presence of basipterygoids and supraoccipital foramina. The Laro-limicolæ, on the other hand, I looked upon as specialised Limicolæ, and they are characterised by absence of basipterygoid processes (in the adult) and supraoccipital foramina, with an increasing tendency to holorhiny or pseudo-holorhiny as they become more and more specialised.

So, in the Rails, regarded by me as specialised gruimorphs, we find a holorhinal condition, absence of basipterygoid processes

Text-figure 5.
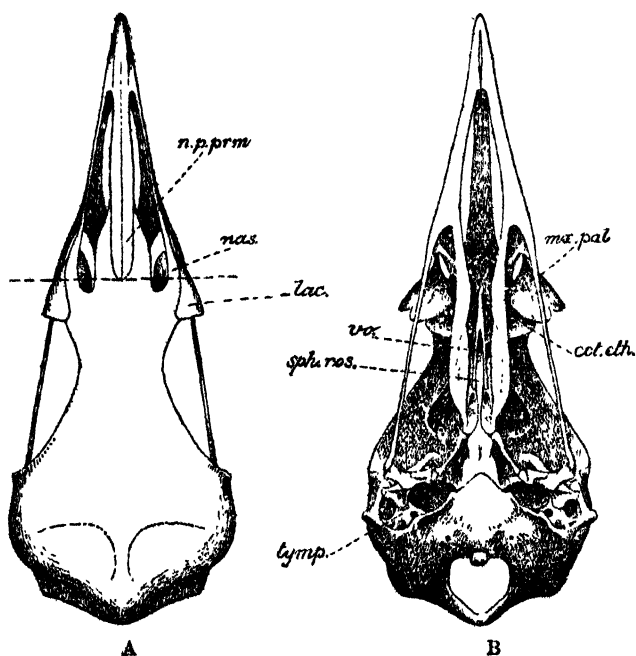
Views of skull of *Mesites*.

A. From above. B. From below.—*n.p.prm.*, nasal process of premaxilla; *nas.*, nasal bone; *lac.*, lacrymal; *mx.pal.*, maxillo-palatine; *vo.*, vomer; *sph.ros.*, sphenoidal rostrum; *ect.eth.*, ectethmoid; *tymp.*, tympanum.

(I have had no opportunity of examining embryos, but in adults, e. g. *Ocydromus*, relics of these are not infrequent), and absence of supra-occipital foramina, while the reverse occurs in the Cranes. I may add that as to the interrelationships of the Gruiformes with the Charadriiformes (more especially with the Scolopacidæ), I am rather sanguine that more light may be gained by further study of the quadrato-tympanic articulation and the tympanic fovea itself.

Lacrymals.—In view of the importance of the lacrymals from

the point of view of classification, the following comparative notes may be useful :—

(1) In the Rails the orbital portion of the lacrymal is not fused with the frontal, and the descending process passes downwards to the maxillo-jugal entirely independent of the ectethmoid and some little way to the front and outer side of it.

(2) In these features the Cranes are ralline, but differ in details.

(3) In *Mesites* the orbital portion of the lacrymal is not fused with the frontal, and the descending process passes down to run very closely along the entire outer border of the ectethmoid ; but it does not really fuse with it, for its identity is never lost. The ectethmoid is quadrilateral, its greatest length being from above downwards. Both the lacrymals and ectethmoids are emphysematous in structure, a gruine or ardeine peculiarity.

(4) In the Parridæ (Jaçanas) the orbital portion of the lacrymals is fused with the frontals, and the descending portion passes downwards and backwards to fuse (but not to lose its identity) with the lower half of the outer border of the ectethmoid, and passes on below it towards the jugal. The ectethmoid is quadrilateral, and the same foraminal space is enclosed by the lacrymals and ectethmoids, as is to be observed in *Mesites*. In fact, the condition in the Parridæ is very like that noted in *Mesites*, except that the orbital portions of the lacrymals are fused with the frontals.

(5) In the Charadriiformes the orbital portion of the lacrymals is fused with the frontals, and whether the ectethmoid is triangular or quadrilateral it is only the terminal end of the descending process of the lacrymal which fuses with the outer angle in the case of a triangular ectethmoid, or the upper and outer angle in the case of a quadrilateral ectethmoid. A very large space is usually enclosed between the lacrymals and ectethmoids.

(6) In *Rhinochetus* the orbital plates of the lacrymals are not fused with the frontals, and the descending process behaves in a way which is very similar to that noted in the Parridæ, but there is just the same hint of a charadriiform note.

(7) In *Eurypyga* the condition is gruine.

So far, then, as the lacrymals are concerned, it will be evident that *Mesites*, the Parridæ (*Parra* and *Actophilus*), and *Rhinochetus* are neither gruine, ralline, ardeine, nor charadriiform in their morphology.

There is, however, one other somewhat important point to be noticed about this region. In any Rail one can easily observe that the upper and inner portion of the ectethmoid is continued forwards and slightly upwards beneath the nasals, and this nasal extension presents a very characteristic turbinate folding of its lower border. These ossified ali-ethmoid turbinates, so characteristic of the Rails and Cranes, are not, so far as I have been able to discover, present in the Plovers, nor, probably on account

of the specialised spongy condition, in *Mesites*, but they can be seen in the Parridæ and in a modified form in *Rhinochetus*.

Finally, as regards this region, it is interesting to note, as indicating how generalised a form *Mesites* is, that the morphology of the lacrymals and ectethmoids in some Pigeons comes very close to that of the form under discussion—in fact, it seems to be an exaggeration of it.

The inter-orbital septum.— This is poorly ossified in *Mesites*, being ralline not charadriiform in this respect.

Sternum.— As Milne-Edwards (*l. c.*) remarks, the keel is so much "cut away" in front that its anterior and lower angle has been carried backwards until it occupies a position which is nearly central as regards the body of the sternum. It is also continued forwards by means of a clean-cut and prominent ridge to effect a junction in the mid-line with the episternal spine (*cf.* text-fig. 6).

Although, so far as I am aware, very little is known for certain of the habits of *Mesites*, it is difficult to resist the conclusion, arrived at by Milne-Edwards, that it is flightless, although the length of its wing-feathers would not seem to preclude the possibilty of some degree of function. For instance, Milne-Edwards states that, although flightless, the bird runs rapidly; so that it doubtless uses its wings in so doing. The carina, however, is not quite so much reduced as in *Ocydromus* or, curiously enough, as in *Rhinochetus*.

On the whole, I think it is safe to say that the general picture of the sternum is ralline. It is certainly more ralline in appearance than that of *Heliornis*, *Rhinochetus*, or *Eurypyga*. If the Parridæ were flightless, I think we should have a remarkably close resemblance to *Mesites*, and the same remark might apply to *Turnix*, although as regards the latter I do not wish to infer anything more than a chance resemblance in two organisms, which are both evidently of great antiquity and considerably generalised. But the sternum of *Mesites* is altogether remarkable for one or two other reasons:—firstly, for the very strongly forked condition of its episternal spine and its very large proportions (*cf.* text-fig. 6); secondly, for the great development of its anterior lateral processes and the fact that four, if not five, ribs are attached to them on each side—a condition which, I think, is unique; and, thirdly, the method of articulation of the coracoids, which is effected by means of two nearly flat and oval-shaped facets set upon two conspicuous and somewhat cylindrical pedicles which rest in high relief upon the body of the sternum (*cf.* text-fig. 6). This also, so far as I am aware, is quite unique among birds, although in the Tinamous there is a suggestion of the same condition. It will be remembered that the Tinamous are great runners.

The flatness or open state of the transverse sternal angle is noticeable in *Mesites*, as apparently is the case in most flightless birds. There is an additional point of interest in this angle in

the fact that, along the whole length of the trough which forms the apex of the angle, a conspicuous degree of cribriform trabecular or cancellous structure exists. This is reminiscent of the Gruine group, and from this potential factor the Cranes may possibly have derived the condition in which the trachea takes a convoluted course down the cancellous tissue of the carina.

Five ribs gain attachment to the sternum in *Mesites* as also in *Rhinochetus*. Six is the general number in the Plovers, seven in the Rails.

The Coracoid.—This is perhaps the most remarkable bone in the anatomy of *Mesites*. Corresponding to the very unusual coracoidal facet on the sternum there is an extremely restricted

Text-figure 7.

Text-figure 6.
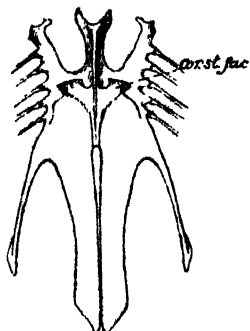
Figure of Sternum of *Mesites*.
cor.st.fac., coraco-sternal facets.
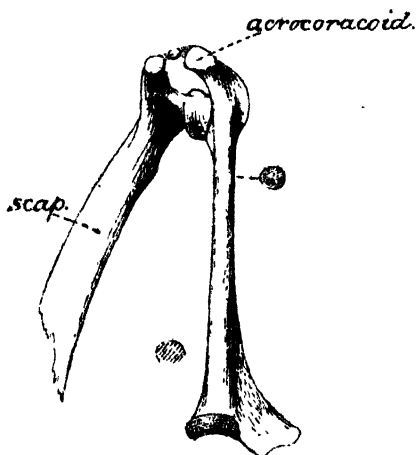
Figure of Scapula and Coracoid of *Mesites*,
showing reduced scapular-coracoidal angle.
Scap., scapula; *acrocoracoid*, acrocoracoid.

coracoidal articulating surface, and from this oval sterno-coracoidal joint the bone passes upwards and forwards as a long and very slender rod-like shaft nearly circular in section. The processus lateralis is poorly developed and sharply demarcated from the thin rod-like shaft. There is no development of a procoracoidal process and no sign of a coracoidal foramen, while the acrocoracoid is also somewhat poorly developed. The peculiarities of this bone do not seem to have impressed Milne-Edwards, and the figure he gives does not correspond in several points to that presented now, a glance at which will indicate how almost unique it is. The total length of the bone is 25 mm., that of the scapula 30 mm., sternum 33 mm. In *Ocydromus* the coracoid measures 33 mm., the scapula 55 mm.,

sternum 50 mm. The skull of *Ocydromus* is twice the length of that of *Mesites*.

The fossil *Phororhacos inflatus* and *Aptornis* are, according to Andrews *, both remarkable for the great length and slenderness of their coracoids. In the case of the former I think this fact is interesting, for not only was it, like *Mesites*, flightless, but Andrews saw points of similarity in its general structure pointing to an affinity with the Gruiformes. The ulna in *Phororhacos* exhibits well-marked tubercles for the attachment of the secondaries. Although flightless, it therefore apparently had well-developed remiges—a condition which exists in *Mesites*.

The Clavicle.—There is not the faintest indication of a clavicle in *Mesites*. It may be noted that Andrews does not mention this bone in his description of *Phororhacos*.

The Coraco-scapular angle.—In view of the fact that *Mesites* is flightless, some increase in the coraco-scapular angle might perhaps have been looked for. Not only is it not larger, but it is actually very obviously smaller than a right angle, measuring in point of fact about 58° or less. In the common Water-Rail it is about 70°. In *Didus* and *Ocydromus* the angle is slightly over 90° (*cf.* Huxley, P. Z. S. 1867, pp. 418 & 425, and Newton, Phil. Trans. 1869, p. 341).

Humerus.—I have compared the humerus of *Mesites* with such forms as *Ocydromus*, *Rallus*, *Porphyrio*, *Heliornis*, *Grus*, *Rhinochetus*, and *Eurypyga*, to say nothing of Plovers, Herons, and other groups. I find that *Rhinochetus* and *Mesites* come much closer together than the rest—indeed, they are very close, especially in regard to the morphology of the head of that bone. *Rhinochetus*, *Mesites*, and *Ocydromus* are all three flightless, and one might have expected a similarity between all three as an effect of that condition; but the head of *Ocydromus* is very different from either of the other two and is typically ralline. In Rails the subtrochanteric fossa is not pneumatic; in *Rhinochetus* and *Mesites* it is, and there is a well-marked foramen in both leading into the cancellous tissue. It is true that this last state of affairs exists in *Grus*, but in *Grus*, with this exception, the general morphology of the head is more strictly ralline. As regards the lower end of the humerus the ectepicondylar process in *Mesites* is barely visible, if at all. The same condition is seen in *Parra*. In the Cranes and Rails it is absent. In the true Charadriiformes it is conspicuous.

Comparative measurements of bones of fore and hind limbs in *Mesites* and *Rallus aquaticus* :—

A. Fore-limb:

	Mesites.	*R. aquaticus.*
Humerus	31 mm.	40 mm.
Ulna	28 ,,	34 ,,
Metacarpo-phalangeal........	27 ,,	39 ,,

B. Hind-limb:

Femur	37 mm.	42 mm.
Tibia	62 ,,	66 ,,
Tarso-metatarsus	41 ,,	42 ,,
Middle toe with claw	39 ,,	49 ,,

Pelvis.—In the Rails one of the characteristic parts of the skeleton is to be found in the pelvis. This is not the place to linger over an enumeration of such characters; but it is a somewhat amazing phenomenon, from the point of view of the persistency of type in any well-differentiated group, to note the extraordinary similarity as regards detail in the morphology of the pelves of two such forms as the Common Rail (*R. aquaticus*) and the Weka Rail (*Ocydromus*), separated as they are by such enormous distances and isolated as the latter must have been for so many thousands of years. This typically Ralline impress cannot be missed throughout the group, even in such specialised forms as *Heliornis* or the Parridæ, which latter are more Ralline than the former in this part of their anatomy. Except as proof of generalization, it is therefore all the more remarkable to note that the pelvis of *Mesites* bears no very close resemblance to the typical ralline pelvis.

It is true that the pre-acetabular portion exceeds the post-acetabular in length, that there is a conspicuous pectineal spine, that the ischiatic foramen is round, and that the postero-external angles and border of the post-acetabular ilium overhang the ischium in a very ralline fashion. Yet the postacetabular portion of the pelvis is much too broad for a ralline picture, and there is not much of the very deep sculpturing of the ileo-renal fossæ so very characteristic of the Rails, nor the marked truncation of the fore end of the ilium, nor the general lateral compression. Compared with the pelvis of other possible allies, there is a general resemblance between *Mesites* and *Eurypyga* or *Rhinochetus*, and it has as much right to be regarded as possessing as many ralline characters as *Heliornis*. I regard the pelvis of the Jaçanas (*M. indicus* and *P. jacana*) as being very distinctly more ralline than that of *Mesites*, and in the pelvis of the latter I can detect no very obvious gruine features, so that the truth may probably be summed up by regarding its features as the expression of a very generalised form—an indication clearly brought out by comparing it with the pelvis of a pigeon, a game bird, a plover, or a button-quail.

CONCLUSIONS AND A PRELIMINARY NOTE ON *Monias benschi.*

Mesites is remarkable for presenting the following associations of characters:—

(1) A complete absence of the furcula.

(2) A very long and nearly cylindrical coracoid with no coracoidal foramen and pronocoracoid.

75*

(3) A remarkable sternum with a very large bifid episternal spine (*Mesites* is Schizognathus), a reduced carina, and coracoidal articular facets whose configuration is, I believe, unique in the class.

(4) A reduction below normal of the coraco-scapular angle.

(5) An over-development rather than an under-development of the sterno-humeral muscles of flight.

(6) Long hind limbs furnished with a full complement of strongly developed muscles.

(7) Feet, toes, and claws which may be described as arboricoline.

(8) Five pairs of powder-down patches and an arrangement of feather-tracts suggestive of a heron (*Cancroma*).

Since writing the above description of *Mesites*, the British Museum has acquired two skeletons of that very rare Madagascan form *Monias benschi* of Oustalet and Grandidier *. It had previously only been known from "skins," and no definite conclusions as to its relationship, other than a suggested connection with the Rallidæ, had been attempted. So far as a preliminary examination permits me to say, I find that *Monias* only differs anatomically from *Mesites* in the following points:—

(1) Its long curved bill.

(2) A shorter tibio-tarsus (the femora in the two species are equal in length).

(3) A shorter tarso-metatarsus.

(4) Longer claws (but the toes are of equal length in the two genera).

(5) A narrower pelvis with shorter pre-acetabular length of ilia and more deeply sculptured ileo-renal fossæ.

(6) Longer wings but considerably shorter ala-spuria.

(7) Ulnar somewhat shorter, although the fore-limb is of equal length.

It is obvious, therefore, that *Monias* must be included in the same family as *Mesites*, and this family must now be known as the Mesœnidæ.

So far as one can judge from the above characters, *Monias* would appear to be more arboreal in habit than *Mesites*.

The possession by both forms of feet, toes, and claws which seem obviously adapted to an arboreal or semi-arboreal life is a point to be emphasised, especially in view of the fact that *Mesites* has been described as a rapid runner, that it is said to be flightless, and that it presents such an extraordinarily contradictory and peculiar complex of anatomical factors, some of which are those usually associated with the mechanism of flight and others with its absence.

* Cf. Hartert, 'Novitates Zoologica,' vol. xix., Dec. 1912.

So far as its systematic position is concerned, most of the anatomical points discussed in this paper show that *Mesites* could hardly be regarded in any other light than as a primitive and generalized form with a decided tendency to Gruiform relationships. At first sight, I was much inclined to regard it as some generalized form of Rail—possibly, indeed, as some primitive form of arboreal Rail ; but further detailed study of this extraordinary bird, corroborated as it has been by a preliminary study of *Monias*, seems almost to force one to the conclusion that the family Mesœnidæ stands entirely by itself, a survival of an early group which cannot be included in any order of present-day birds. Into this question—which, of course, implies the creation of a new order Mesœnæ for its reception—I shall hope to go in the near future.

In relation to the possible semi-arboreal life of *Mesites*, I should also have liked to have discussed here the possibility that, in addition to its cursorial propensities, it may possess some additional factor of gliding or planing flight. This is suggested by the strangely elongated coracoid, and its possible use as some sort of a supporting strut to enable the wings to be held extended in the manner of a monoplane.

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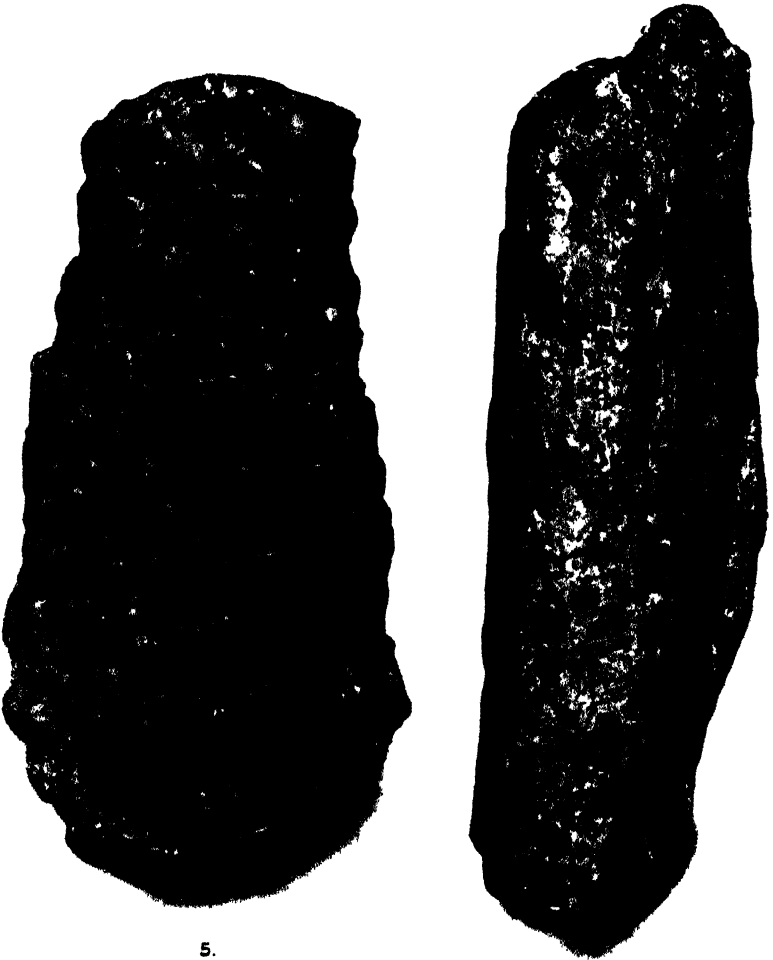
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ON THE BURROW OF THE RODENT SPALAX (MESOSPALAX)

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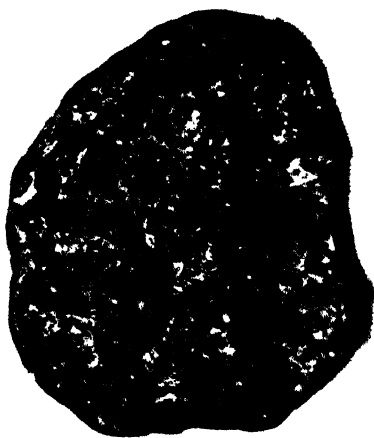
ON THE BURROW OF THE RODENT SPALAX (MESOSPALAX)

52. On the Burrow of the Rodent, *Spalax* (*Mesospalax*).
By IVOR MONTAGU, F.Z.S.

(Plates IV., V.; text-figures 1–4.)

Introduction, and Summary of previous Work.

In September 1924, Ivor Montagu and Bancroft Clark, while engaged in collecting mammals, spent five days in Hódmezővásárhely, South Hungary, trying to catch *Spalax* (*Mesospalax*) *hungaricus* (according to Dr. Éhik, the *Spalax* found there is referable to this species). They were unprepared with material for the exact reproduction of tunnel systems or the quantitative examination of the contents of tunnel chambers, and it was only after some two hundred metres of burrow had been excavated, without any capture being made, that careful observations were begun.   The writer acknowledges the more than courteous assistance of everyone with whom he came in contact during the course of the work, especially Mr. Béla Bodnár of the Budapest Anatomical Institute, and the brothers Kriván of Hódmezővásárhely, who prepared casts of the burrows.

The literature of *Spalax*, though rich with study of the morphology and systematics of the genus, is nearly without details of its living habits.   Anderson, in "*Spalax typhlus* in Africa," P.Z.S. 1892, p. 473 (1), describes his hunting of *Spalax* (now *Microspalax*) in Egypt.   He says that the burrow system appears to have the form of a great number of tunnels, often branched, radiating out from a nest placed 4 feet deep; that some tunnels are short and deep, others run above these; that he found, in the single system excavated, two domed food-chambers, one empty, the other containing some 68 small bulbs.   He describes the tunnels as perfectly smooth, clean, and cylindrical; and supposes that they are made in search of food, since those near the surface pass bulbs like those found in the store-chamber. The ground above such a system was covered with small mounds of earth.   It seems that the soil must have been very easy to work in and soft, since his work, which was crowned with the capture of three specimens, and in the course of which he opened up burrows for a distance equal to that which occupied Montagu and Clark for three days, took only four hours.

Loisel, in " Observations sur *Spalax monticola serbicus* faites en Serbie," Bull. Mus. H. N. Paris, 1916, p. 71 (2), records a number of observations on *Mesospalax*.   He declares that the animals dug with the snout (*groin*) and front feet.   He says that the burrows are circular, *assez superficielles*, usually some 6 or 7 cm. deep, and that, when the animals are making them, one can follow them with the eye by the movement of the earth.   He says that *Spalax* sometimes borrows the galleries of the mole,

Text-figure 1.

Section B.

Section L begins
5 yards in arrows direction

Cultivated field

Path

Path

ha-ha
5 ft. deep
4 ft. wide at top

Section A

Scale Yards
0   5   10

Fig 1 General Vertical Plan

Text-figure 2.

Fig 2 Section A Horizontal Aspect.
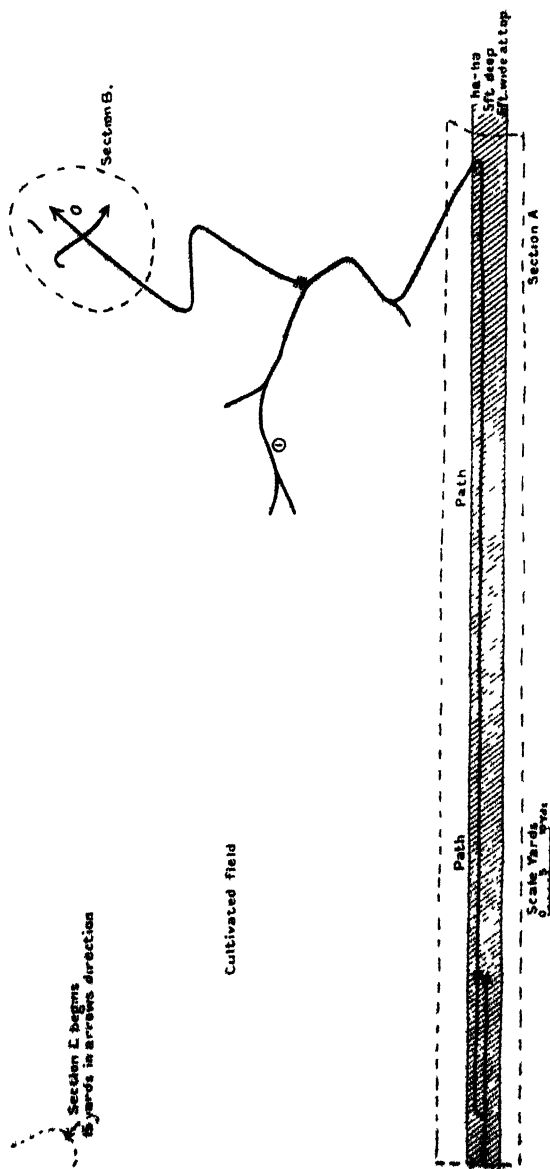
and describes three kinds of chambers: (a) a sleeping-chamber
1 m. deep in summer, or more in winter; (b) a store-chamber;
(c) a chamber, au sol de terre battu, to receive and hold rain-
water. He records the frequent occurrence of the animal in
vegetable gardens, and says that, besides root-crops, its strictly
vegetarian diet includes surface-crops (he found such in its
stomach), and that, having fed on these latter, it stops up the
surface-hole in returning to the burrow. He kept specimens
alive, but thinks it impossible to do so successfully for more than
five days.

From the evidence brought forward by Montagu and Clark
it appears that *Mesospalax* differs from *Microspalax* in con-
structing highly specialised burrows, packing the excavated earth
into the sides instead of merely shifting it on to the surface, and
that Loisel's observations are, on other points also, incomplete or
inconclusive. Méhely and others have inclined, on morphological
grounds, to infer a progressive specialisation for underground
life leading from the southern *Microspalax*, through the central
Mesospalax, to the northerly (the South Russian) *Macrospalax*.
The habit-differences between the Hungarian *Spalax* and
Anderson's Egyptian form tend to confirm this view; an account
of the habits of the Russian form would be of special interest.
Such a one by Charleman, in " Mammals of the Neighbourhood
of Kiev," Mat. Pozn. Jaun. j–z. 1915, p. 75 (3), appears to exist,
but is not at present accessible.

ILLUSTRATIONS.

I. Scale-diagrams of the burrow system.

Text-fig. 1. *General Plan*:

The cultivated field contains: melons, maize, sunflowers,
tomatoes, paprika, pumpkins, cucumbers, beans, potatoes,
radishes, carrots, parsnips.

Average level of burrow centre 4″ below nearest earth-
surface.

(1) parsnip-plants growing here, three gnawed.

//// isolierung 4–6″ thick.

Arrows indicate unfollowed continuation.

Text-fig. 2. *Section A*:

Figures indicate, in inches, depths of tubes into side,
or below bottom, of ha-ha.

Where no figure, tubes run average depth 4″ below.

(2) dung-chamber containing fresh moist dung and, in
it, fly larvæ.

(3) 5 or 6 parsnip-roots earth-embedded, in one case as
an isolierung 1″ from the entrance to a deep chamber.

(4) nest.

///// isolierung 4–8″ thick.

Arrows indicate unfollowed continuation.

Text-fig. 3. *Section B* :

(4) nest.

Arrows indicate unfollowed continuation.

Figures indicate, in inches, depths of tubes below field-surface.

— — — extent of excavated pits.

In digging pit to follow main burrow, running from 9 o'clock, several connections were probably lost.

Text-figures 3 & 4.
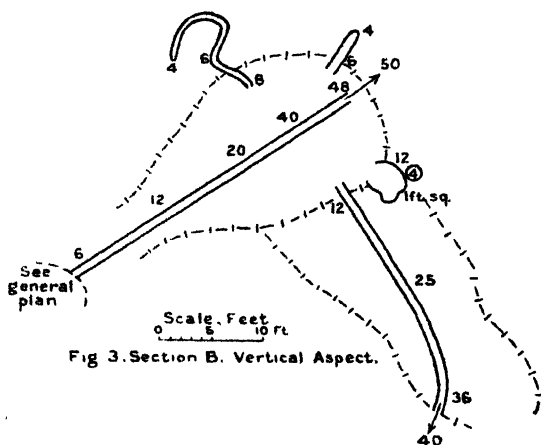
Fig 3. Section B. Vertical Aspect.

Scale. Feet
0   5   10 Ft
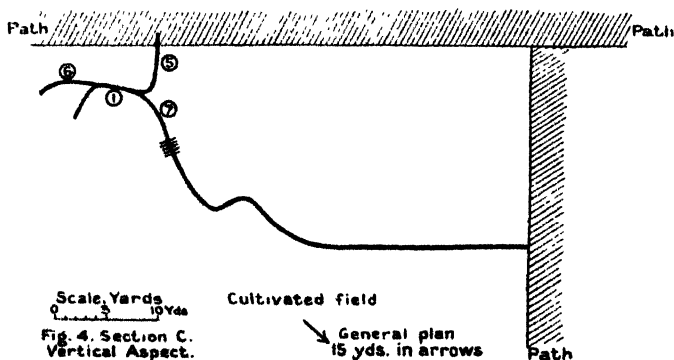
Fig. 4. Section C. Vertical Aspect.

Scale. Yards
0   5   10 Yds

Cultivated field

General plan 15 yds. in arrows direction.

Text-fig. 4. *Section C* :

Average level burrow 4–6″ below field-surface.

(1) Three gnawed parsnip-plants.

(5) Microtus.

(6) Snake.

(7) Lizard.

///// isolierung 4–6″ thick.

II. Casts of parts of the burrows.

The negatives are shown. These, with positive copies, have been presented to the British Museum (N.H.) by Montagu and Clark. Other positive copies have been similarly presented to the Natural History Museum, Vienna ; the National Museum, Budapest ; the University Museum, Szeged ; and the Gymnasium Museum, Hódmezovásárhely.

Pl. IV. Fig. 5 :
> Wide bore (usual) from side of ha-ha ; showing nose-marks.

Pl. IV. Fig. 6 :
> Narrow bore (infrequent, except in very deep tubes) from side of ha-ha ; showing nose-marks rubbed flat.

Pl. V. Figs. 7 and 8 :
> From system fig. 4 on side of isolierung proximal to gnawed roots ; showing little nose-work, tooth-marks (of divaricated lower incisors).

Pl. V. Figs. 9 and 10 :
> From system fig. 4 on side of isolierung distal to gnawed roots ; showing fine nose-work.

Deductions from Illustrations, and other Observations.

A. *Local Distribution.*

The animal is common in the neighbourhood of Hódmezo-vásárhely. Within the last few years it has noticeably extended its range westwards. It is still restricted to the fields to the east of the town, being absent from the west, north, and south. The appropriately placed farmers are familiar with it ; they frequently encounter its burrows and, at rare chance, turn up specimens with the plough. By intention the animal is also difficult to catch. Digging for it is made uncertain of success by the heaviness of the soil, and by barriers (Isolierungs) which interrupt the continuity of the burrows and hinder the unravelling of each system. In the last twelve months six specimens have been taken, four by farmers and two, after three weeks' digging, by Mr. Bodnár.

B. *Nourishment.*

Spalax is quite easy to keep alive in captivity. Dr. Éhik kept a specimen in the National Museum, Budapest, for some time, and afterwards sent it to America.

Nothing was noticed which could be described as an access to the surface, stopped-up or otherwise. Indeed, in the whole course of the excavated tunnel system, only at two points was it possible to infer the presence and position of a tunnel by surface-observations. At each point the dead and draggled appearance

of parsnip-plants indicated that a tunnel ran beneath them, their roots having been gnawed off and carried away or eaten (figs. 1 & 4). The writer does not regard the absence of positive evidence as being sufficient to deny that *Spalax* may, here as in Serbia (Loisel, 2), supplement its diet with surface-plants; but, in this connection, it should be noted that the animal is accused by the local farmers only of ravaging root-crops.

C. *The Digging Method of* Spalax.

Loisel's statement (2) that the animal digs with its *groin* and fore paws can be regarded as an approximation. The feet are perhaps used to scrape clear the loose earth, but the excavation itself is carried out by the teeth, as has been observed by Dr. Éhik. Unlike those of the mole, the fore paws of *Spalax* are scarcely more specialised as digging organs than are those of *Mus* or *Rattus*. The actual chiselling off of the earth is carried out by the incisors of the lower jaw. The tooth-grooves, when seen, rarely (figs. 7 & 8), on the tunnel-wall, are paired and clearly identifiable as having been made by these teeth, the tips of which are slightly divaricated, in contrast to the tips of those of the upper jaw, the inner edges of which are in close congruence.

The animal finally completes the burrow by packing the loose earth into the walls with powerful and tremendous thrusts of its horny padded nose. No excavated earth whatever is to be seen upon the surface, the tunnels are usually some four inches in diameter and may be four feet deep, and, consequently, it is clear that an advanced degree of specialisation is to be inferred from the feat involved in packing. The walls are thus so firmly built that they form a close consistent mass, breaking much less readily than the surrounding earth, and showing evenness, like plasticine, when shredded with a knife. The great hardened nose-cap prints itself into this process into the earth and leaves the muzzle-outline, an almost omnipresent identity-mark in the tunnels, which appear pitted as by some great pox (figs. 5, 9, & 10).

In fig. 4 is illustrated an extension of the animal's residence-tunnel in search of food. The food being found, at point (1), possibly aware that a surface-trace of its depredations was inevitably left in the form of the dead parsnips, the *Spalax* returned to its residence-tunnel, the walls of which are well packed (figs. 9 & 10), and closed off the forage-tunnel with an isolierung, leaving the walls of the extension scarcely packed, and some of the original tooth-marks unobscured by heavy after-work of the nose (figs. 7 & 8). That the animal was not inhabiting the rough unfinished tube beyond the isolierung is additionally suggested by the presence there, probably led down by intersecting mouse-holes, of a *Microtus*, a lizard, and a snake.

Where, perhaps, for some reason connected with the confor-
mation of the soil, the bore of the tube is exceptionally small
(fig. 6), the constant passage of the animal has worn the nose-
prints nearly out. They are barely discernible beneath a general
rubbed flatness.

D. *Special Structures of the Burrows.*

The word isolierung has been coined and several times used
above, maybe with insufficient explanation. It denotes a barrier
of earth set in a tunnel and, from whichever side approached,
making the tunnel-tube appear to end blindly. Such a structure
may make one miss a branch, or desist from following a straight
tube, when excavating with hand tools, or even, in hard ground
or deep, when using a spade. The possibility of its occurrence
makes it necessary to dig an area much wider and deeper than
the actual burrow system, and even then destroys certainty that
the exposed system is entire.

The only true chambers, in the sense of excavations wider than
the tube bore, are the sleeping-chambers. Each of those seen was
a cavity about twelve inches in diameter and some four or five
inches high; one had a smaller hole, about two inches high and
deep, opening into it. In both cases the cavity was loosely
packed with bedding, chiefly dried grass (evidence of a sometime
surface sally); in the one case more carefully examined, the
outer leaves of onion bulbs also formed part of the bedding. In
this, the nest in the ha-ha, were fragments, several quite large
(2 cm. by 1 cm.), uncertainly identified as *Unio*-shell. The
presence of these is intriguing. The source from which they
reached the *Spalax* may have been manure; but the circumstances
of their position in the nest, deep, distant from the cultivated
soil, some way from any food, strewn on the carefully kept hard
earth floor beside clean dry bedding, these suggest purpose, such
as that of the American "Trade Rat," rather than accident.

Loisel's water reservoirs (2) were not seen. The food-stores
and dung-chambers are described in the notes to fig. 2. The
burrow-tubes were perfectly clean and empty throughout, except
those, blind-ended, to which the names above have been given.
No fleas were anywhere found in the burrow; dung-flies, probably
attracted by warmth on their way to and from the adjacent
dung-chamber, were present in the nest in the ha-ha, and perhaps
unable to get to the surface owing possibly to the closing up of
the hole by which their parent entered.
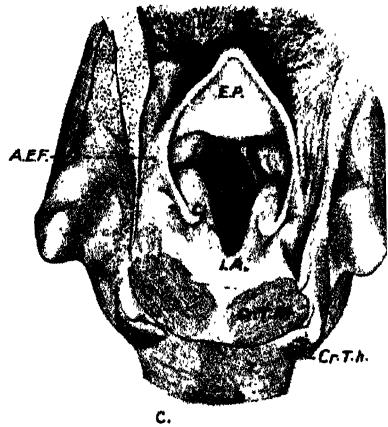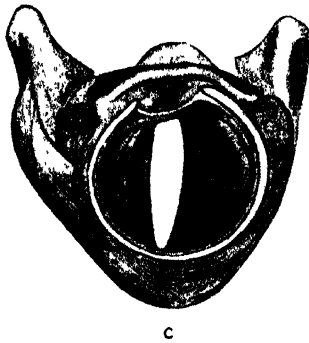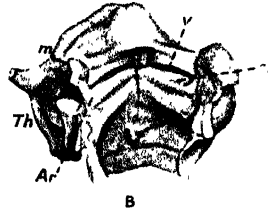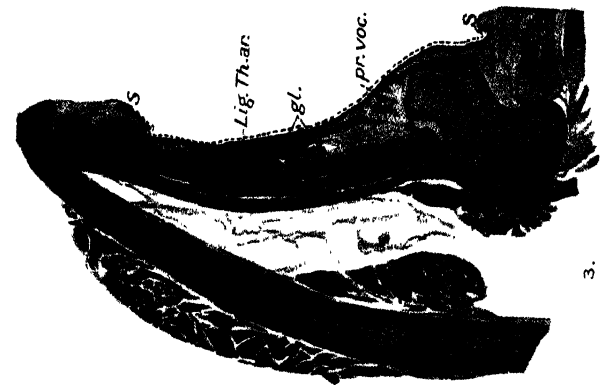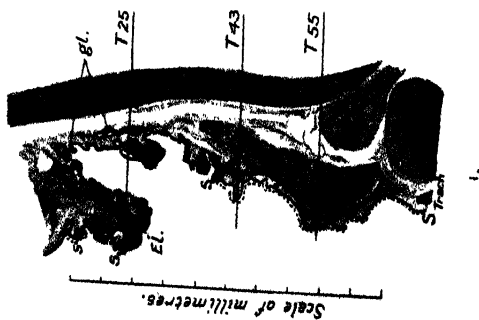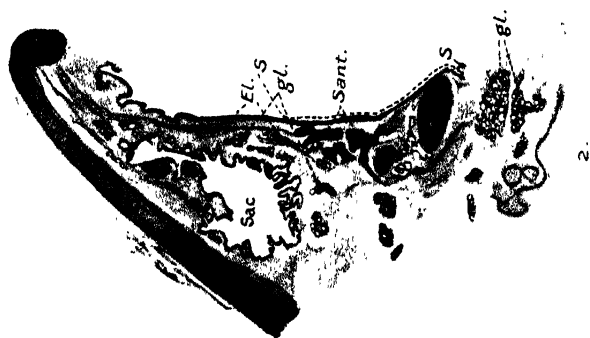
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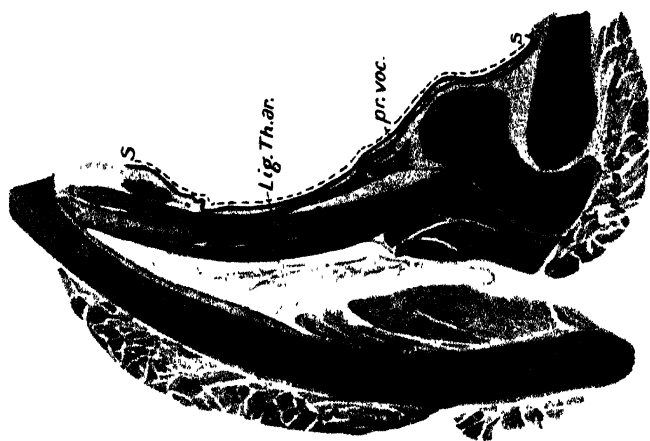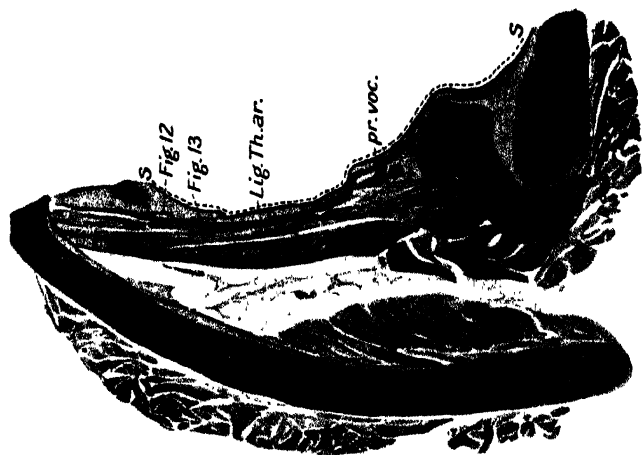
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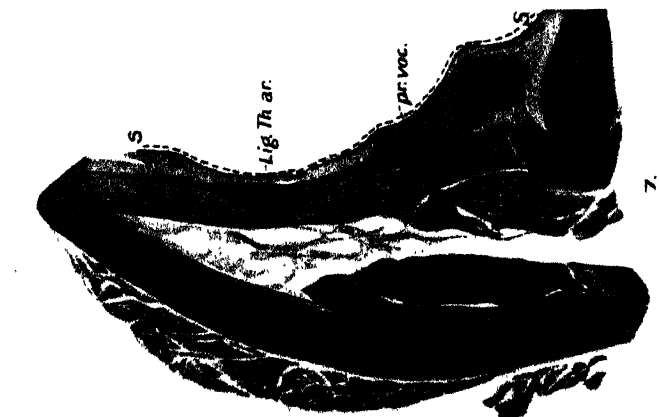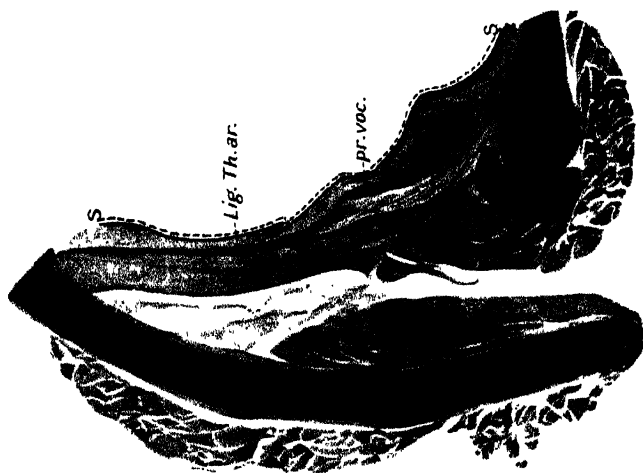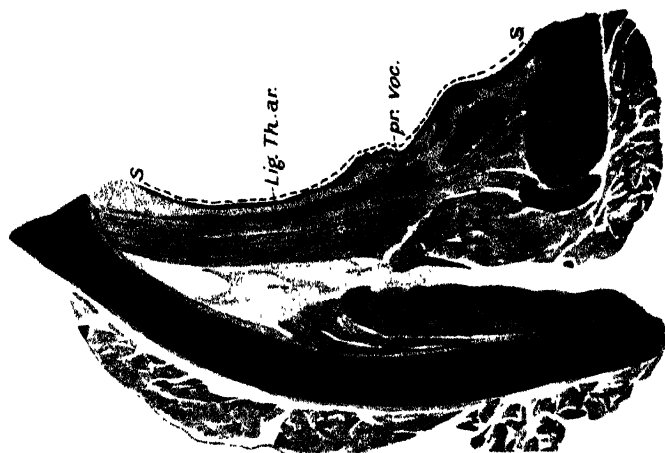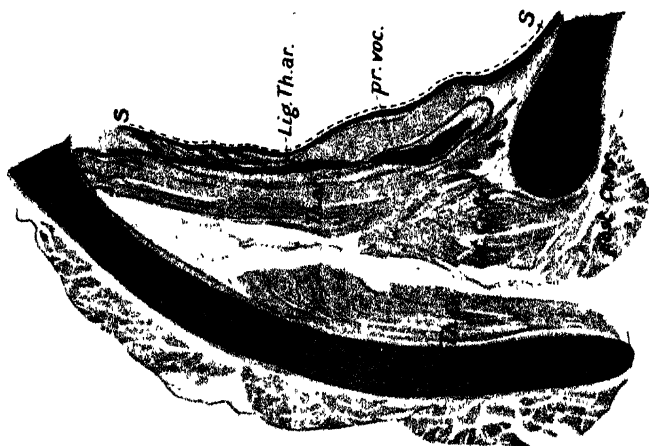
Thy. Ar. int.   El. v.c.

Scale of tenths of a millimetre

12.

John Bale Sons & Danielsson Ltd

Lig. Th. ar.

pr. voc.

S.

S.

S.

S.

S.

10.

11.

LARYNX OF HYLOBATES SYNDACTYLUS.

53. A Study by Serial Sections of the Structure of the Larynx of *Hylobates syndactylus* (Siamang Gibbon). By Sir FREDERICK MOTT, K.B.E., F.R.S., M.D., LL.D.*.

(Plates I.-V.)

CONTENTS.

1. INTRODUCTION.

In the year 1911, in conjunction with Dr. Edward Schuster and Sir Charles Sherrington, I investigated the " Motor Localization in the Brain of the Gibbon, correlated with an Histological Examination." The results were published in the ' Proceedings of the Royal Society ' of that year.

The animal used for the experiment was *Hylobates syndactylus* or Siamang Gibbon ; it was a male, about 3 feet 6 inches in height, with black smooth hair ; " it was remarkably agile ; when standing or running on the ground it maintained almost an erect posture, using its long arms to balance itself very much as a man would walk on a tight rope with a balancing-pole. It was kept for some days before the experiment in the animal rooms of the Physiological Laboratory, Liverpool University, and it was frequently heard to utter vocal sounds of very varying pitch and quality : thus it could imitate the shrill high-pitched whistles of the guinea pig and the relatively low-pitched bark of the dog."

Having regard to the aforesaid vocal powers of this animal, I thought it would be interesting to make a careful examination by serial sections, horizontal and vertical, of the larynx in order to ascertain the structural conditions which could explain the loud sounds the Gibbon has always been accredited with emitting, and the great range of pitch this particular animal was able to effect when it imitated the " low-pitched bark of the dog and the shrill high-pitched whistle of the guinea-pig." The larynx was carefully dissected to show the extrinsic muscles and their attachments. Drawings were made to show the naked-eye anatomical features ; the larynx was then divided into halves through the middle line, and these were prepared for cutting serial sections by the celloidin method. This mode of investigation was employed in order that all the parts should remain in their proper position.

2. Literature.

Darwin in his 'Descent of Man,' page 527, states : "The voice of the adult male gorilla is tremendous, and he is furnished with a laryngeal sac, as is the adult male orang. The Gibbons rank among the noisiest of the monkeys, and the Sumatra species (*Hylobates syndactylus*) is also furnished with an air-sac ; but Mr. Blyth, who has had opportunities for observation, does not believe that the male is noisier than the female. Hence, these latter monkeys probably used their voices as a mutual call." These animals live in dense forests, and, although they can assume the erect posture, their mode of progression is by swinging themselves by their long arms from branch to branch of trees. In Brehm's 'Thierleben' it is recorded that a Hoolock Gibbon in the London Zoological Gardens appeared to have the best-sounding and best-tuned voice of any animal except man. Dr. Sonntag, in his recent work 'The Morphology and Evolution of the Apes and Man,' page 69, remarking upon the habit of the Gibbons, states :—

"The Gibbons are gentle affectionate creatures, but there is evidence that they bite severely when they are irritated. They are also very timid, and the sight of an enemy makes them take refuge in flight.

"Their *vocal powers* are considerable, and their penetrating cries are audible for miles. Dr. Salomon Muller, an observant and careful naturalist, in describing the voice of the Siamang, said, 'the voice is grave and penetrating, resembling the sounds gŏek, gŏek, gŏek, gŏek, gŏek, ha ha ha ha haaaäñä, and may easily be heard at a distance of half a league.' Martin described the cry of the agile Gibbon as 'overpowering and deafening in a room, and, from its strength, well calculated for resounding through the vast forests.' Pocock contrasted the voices of the Hainan and Hoolock Gibbons as follows : 'The voice of our Hainan Gibbon is quite different from that of the Hoolock. It is a high-pitched trill all on the same note, and shriller even than the high note of the Hoolock's cry. It consists of about three to six distinct cries repeated in very rapid succession, suggesting almost production by vibration of the tongue, although, as a matter of fact, I believe the lips alone are instrumental in producing the effect. There is then a momentary pause, after which the cry is repeated. It may, perhaps, be represented in the following way : 'hoo hoo hoo hoo-hoo hoo hoo-hoo hoo hoo hoo hoo, etc. The Hoolock, on the contrary, cries as follows : hūh, hōō, hūh, hōō, hūh, hūh, hōō, hūh. The "hōō" is on a lower note than the "hūh," with which the cry frequently ends. The ordinary expression of anger or remonstrance in the Hainan Gibbon is a prolonged and guttural grunt, repeated rapidly and often, and frequently interspersed with a kind of warble when the excitement rises.'"

I am indebted to Dr. Edward Schuster for the very accurate

and beautiful series of drawings, without which this communication would be of little value, and to Dr. Chalmers Mitchell, F.R.S., for kindly consenting to their reproduction in the ' Proceedings of the Zoological Society.'

Giacomini * has given an account, of which the following is a translation :—

"'There was no trace present of the laryngeal sacs seen among the other Simidæ. When the larynx was opened and examined on its inner face the vocal cord was found to extend for a length of 4½ mm. in its free portion. Anteriorly the ventricular fold is some way distant from the vocal cord, but it approaches it near the posterior end. In this way the entrance to the ventricle of Morgagni appears wider anteriorly than posteriorly. The ventricle is not very deep but it extends backwards beyond the cord.

"(M Section). The cord has a rounded margin, which stretches upwards and inwards. It is composed essentially of compact fibro-elastic tissues with few blood-vessels; there are no papillæ .... It is covered with stratified epithelium on its free surface.

" Passing upwards and outwards from the cord one meets a groove which forms the floor of the laryngeal ventricles, and at this point the epithelium changes to the columnar and its surface also is modified. While that portion which clothes the cord is smooth and even, here it is raised up into crests and villi. ...

" The sub-glottidean portion of the mucosa which stretches from the cord towards the trachea is regular, being raised up only into one light convexity which corresponds with the base of the thyro-arytenoid muscle. ...

" In the mucosa of the larynx of the Gibbon the mucous glands are neither numerous nor voluminous, and are confined to the walls of the ventricle. They have the ordinary disposition and conformation. The most inferior of the small glands are situated at the point in which the wall of the ventricle joins its floor. The cords are without glands, and glands are lacking also in all the sub-glottidean portions of the mucosa, commencing to reappear only when the trachea is reached.

" This arrangement of the glands is somewhat singular, and contrasts with that observed in the Gorilla, where in this region the glands are more voluminous and nearer to one another.

" The thyro-arytenoid muscle appears in sections as a long and slender cone, with its rounded base below and its apex tapered off above. The base extends far below the vocal cords, and pushes the mucous membrane slightly inwards as if simulating the hypoglottidean fold of the Gorilla.

" The internal surface of the muscle is in relation with the mucosa; running in correspondence with the vocal cord it recog-

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* Giornale della R. Accademia di Medicina di Torino, 1897, iv. 7. 9, p. 649, etc.

nizes its presence (risente la sua presenza), and sends out a
slender vocal extension which is directed towards the base of the
vocal cord --without, however, reaching it. The fact is clearly seen
in the more anterior sections; joining the middle part of the
cord at the point of the muscular extension there is a small
bundle of fibres, marked (colpite) at right angles to their course
(striated?), as in the remainder of the muscle, which represents
the prolongation which has been rendered independent of the
body of the muscle.

"I consider that this arrangement is most interesting, because it
demonstrates that in the Gibbon the vocal prolongation of the
thyro-arytenoid muscle begins to be indicated. This condition is
characteristic of the human larynx, but no trace of it exists in
the Gorilla.

"The apex of the thyro-arytenoid muscle terminates a little
above the upper extremity of the ventricle of Morgagni. But a
little anteriorly (presumably anteriorly to the section figured),
this apex, composed of a few fibres, may be followed higher
up, as far as the superior margin of the thyroid cartilage.
where connective-tissue fibres, combinations of the muscle, are
inserted.

"The ventricular fold (superior vocal cord), only slightly
developed in height, is built up as in the other examples; but
those muscular fibres which we have said constitute the muscles
of the false vocal cord are absent. The muscular fibres which are
observed in the section above its base do not belong to the fold,
but are a portion of the aro-epiglottic muscle."

Giacomini gives the following series arranged in order of degree
of resemblance to the white man, and with regard to the con-
formation of the larynx, from his own researches :—

> White man.
> Negro woman.
> Bosch man.
> Chimpanzee.
> Gibbon.
> Macacus.
> Cercopithecus.
> Gorilla.
> Orang.

3. NAKED-EYE ANATOMY.

The accompanying drawings (Pl. I. figs. 1, A and B) show
the following structures (natural size) :—

Plate I.

> A. Natural size. Dissection from dorsal surface. The cartilages have been
> partially cleared of muscles, etc., on the left-hand side. The anterior
> border of the thyroid cartilage had been cut away previously on the right-
> hand side.

B. As above, the cricoid cartilage has been divided in the middle line, and the larynx spread out to show the true and false vocal cords, etc.

TH. Thyroid cartilage.   AR. Arytenoid cartilage.
CR. Cricoid cartilage.   V. Ventricle.
C. Vocal cord.   AR. Arytenoid cast.

The larynx, after dissection, was divided into two halves. The left-hand half was cut into a series of sections 10 mm. thick in a vertical plane, while the right hand half was cut transversely. Every fifth section in each series was mounted and stained by hæmatoxylin and eosin or Van Gieson stain and mounted in Canada Balsam.

Plate 1.

C. Drawing showing the glottis as seen from above, magnified two-and-a-half times. The dorsum of the tongue (D.T.), and behind this the epiglottis (E.P.), extending from the rim of it is the aryteno-epiglottidean fold of mucous membrane, which posteriorly curves forward over the cornicula and the arytenoid cartilages and backwards over the interarytenoid muscles. In the mid-line is a black surface representing the part of the tracheal lumen which is visible; this is bounded on each side by two sharp edges (vide fig. 2, D, for each explanation), and above and outside are again two apparently sharp edges seen; these are the edges of the true vocal cords. Outside and above these, on either side, are the entrances to the ventricles of Morgagni, and lying above are seen, on either side, a roundish swelling of mucous membrane constituting the false vocal cords, covered where they come in contact with squamous epithelium, and containing in their interior a sacculus (vide fig. 2, Section 25).

D. Drawing looking up the cut trachea and showing the infolding of the mucous membrane at its junction with the cricoid cartilage (vide fig 1, Section L, 31; and fig 10, Section T, 52). The tracheal rings are seen internally. Magnification two and-a-half times.

Further observations on the naked-eye anatomy were made from the series of sections stained by hæmatoxylin and eosin. The elastic fibres could be easily seen in horizontal section as a blue purple-stained thread stretching from the processus vocalis behind to a little nodule of elastic fibro-cartilage in front and even a little beyond it —almost, indeed, to the angle of the thyroid cartilage in which the thyro-arytenoid muscle stained pink ends. The cartilages are stained a purple-pink. It was thus easy to measure accurately the length of the vocal cords in these sections.

From the tip of the processus vocalis to the attachment of the thyro-arytenoid muscle at the angle of the thyroid cartilage measured 1 cm.; the free edge of the vocal cord measured 0·6 mm. From the angle of the thyroid cartilage to its posterior border the maximum measurement was 2 cm.

4. MICROSCOPIC ANATOMY.

Fifty serial sections from above downwards (termed vertical) were examined. Fig. 1, section L. 31, is a drawing showing anatomical points of interest. The extent of squamous epithelium S.-S. is shown by the dotted line, and it will be observed that it extends from the first ring of the trachea to the lower border of the ventricle of Morgagni, above which there is columnar epithelium and very irregular outlines; beneath the mucous membrane are numerous mucous glands, *gl.* There are also some nodules of lymphoid tissue. On the false vocal cord there are two surfaces covered with squamous epithelium S.S., and there are numbers of elastic fibres, E.L., in its structure. It is probable that squamous epithelium marks the situations where the false cords come in contact. A series of 55 horizontal sections were examined, of these three sets of horizontal sections represented in Drawings T. 25, T. 43, and T. 55 will be first considered in relation to the three levels in the vertical section L. 31. Between the levels T. 43 and T. 55 elastic fibres are distinctly seen. T. 55 marks the thickest point of thyro-arytenoid muscle. Just above the level of the upper border of the squamous epithelium S, the thyro-arytenoid muscle terminates in a blunt conical edge.

Serial Horizontal Sections.

Fig. 2, section T. 25, shows the saccula, and from this we can understand the appearance presented by the false vocal cord in Pl. I. figs. B & C, and how if it were filled with air—by virtue of the numerous elastic fibres its inner wall possesses—it could be so distended as to cause approximation of those surfaces of the false vocal cords which are covered with squamous epithelium; also that covering the cornicula and apices of the arytenoid cartilages entering into the formation of the aryteno-epiglottidean fold would be approximated during adduction of the vocal cords.

Fig. 3, T. 43, shows the elastic fibres of the vocal cord extending from the processus vocalis, *pr.voc.*, of the arytenoid cartilage to end in the tendinous attachment of the thyro-arytenoid muscle. A little nodule is seen just inside of S, where the squamous epithelium ends and a small gland appears. This nodule consists of elastic fibres and a few cartilage cells; it resembles the cartilages of Santorini in its structure. S.S., squamous epithelium, shows the parts which are approximated in adduction. A considerable-sized mucous gland, *gl.*, is seen in the fibrous tissue between the vocal cord and the thyro-arytenoid muscle, *th.ar.* The more extensive attachment of the muscle to the arytenoid cartilage is seen at this level. Fig. 4, section T. 46, shows the same structures as in fig. 5.

Fig. 5, section T. 47, shows the nodule of elastic fibro-cartilage seen in 43—it has disappeared in section of the series,

fig. 7, T. 49. This nodule marks the position of the muscle-fibres which are inserted into the vocal cord, figs. 12 & 13, as shown in the situation indicated in fig. 6, T. 48. The connective tissue forming the perimysium and endomysium of the fibres of the thyro-arytenoid muscle terminate by gradually passing into tendinous fibres which are inserted into the angle of the thyroid cartilage—this tendinous fibrous tissue surrounds the nodule of elastic fibro-cartilage. No nerve-endings were seen in this tendinous tissue, but it is quite possible that they exist and could be demonstrated if appropriate staining methods had been employed. In the two marked areas 12 and 13 there is a band of muscle-fibres which terminate by rounded ends in a tendinous structure which intermingles with the band of elastic fibres of the vocal cords. The endomysium is continuous with this tendinous tissue; in the tendons of the eye-muscles there are special proprioceptive kinæsthetic nerves and their endings which are excited when the muscle-fibres contract. It would be of interest to ascertain if there are sensory nerve-endings in the tendon of the thyro-arytenoideus muscle. There are none in the vocal cord itself. The slender band of muscle-fibres inserted into the anterior third of the vocal cord is the thyro-arytenoideus internus or vocal muscle found in the human, but not, according to Giacomini, in the Gorilla.

Fig. 12, Pl. V. shows this muscle and its insertion into tendinous tissue intermingling with that of the elastic fibres of the vocal cord.

Fig. 13, Pl. I. shows the muscle-fibres with rounded ends terminating in a definite tendinous cap.

Figs. 7–11, T. 49 55, show the changes of appearances in the cartilages, muscles, and the vocal ligament at different levels. It will be observed that the thyro-arytenoid muscle becomes thicker as we descend the levels, and that along its whole border in each level there is a band of elastic fibres, and that squamous epithelium covers the free surface of the thyro-arytenoid ligament (vocal cord). The lateral crico-arytenoid muscle increases in size also and is largest where the arytenoid cartilage is hardly visible. In dissection the crico-thyroid muscle was found to have fibres arising from the first ring of the trachea. This development is no doubt to enable the tracheal aperture into the larynx to be narrowed during vocalization, and that is why we find in this movable part squamous epithelium extending to the mucous membrane over the top of the 1st ring of the trachea (Pl. II. fig. 1).

5. The Correlation of Structure and Function.

The structural characteristics of the larynx of this Gibbon explains the capacity these animals have of emitting very loud sounds.

Thus the extension downwards of the thyro-arytenoid ligament (fig. 11, T. 55) and its infolding to form a sharp edge on either side with a narrow slit (*vide* Pl. 1. fig. 2 A & B), so that the true vocal cords could only be seen from below when there was complete adduction by bipolar stimulation, is obviously an arrangement by which an increased pressure in the trachea is obtained by diminishing the area of impaction of the column of propelledair on the vocal cords (*vide* figs. C, D, Pl. I.; fig. 1, Pl. II.). The loudness of sounds is increased proportionally to the amplitude of vibrations of the vocal cords, which is dependent upon the force with which the air is expelled through the chink of the giottis. The animal can by filling its laryngeal sacs bring into play the false vocal cords, which by their approximation necessitates a still further increase of propulsive force before the air can escape and set in vibration the vocal cords—in fact, the animal, when it wishes to emit a loud sound, can employ the "coup de glotte" of the singer. "This ‘glottic shock’ is produced by two muscular folds called the ventricular bands, or false vocal cords, which in conjunction with some other muscles cause a complete constriction of the air-passage above the true vocal cords. Their function is to protect the larynx during swallowing and to take any strain exerted by the respiratory muscles during effort, such as *rigorous action of the arms* or abdominal muscles involving the fixation of the chest. Thus action in coughing is of the nature of a spasm preceding an explosion of the breath"—Aikin. W. A., ‘ The Voice : An Introduction to Practical Phonology.’ Such powers of emitting a loud vocal call of warning or of sexual attraction must play an important part in the self-preservation and preservation of the species of these timid, agile, arboreal animals. Doubtless, when this particular Gibbon imitated the low-pitched bark of the dog he employed the whole of the vocal cord, but how did he imitate the shrill whistles of the guinea-pig ? In order to imitate the shrill whistles of the guinea-pig it may be assumed that the animal employed some means of considerably shortening the vocal cords and permitting only their free edge to vibrate, as in the human high soprano or falsetto voice in the male. This in all probability the animal was enabled to do by the thyro-arytenoideus internus, which we have seen ended obliquely by a tendinous insertion into the anterior third of the vocal ligament (*vide* figs. 12 & 13). When the vocal cords are tightly compressed together by the adductors, the vibrations at their back ends in the neighbourhood of the vocal processes are interfered with by compression or "stopped." The result is that only the anterior parts of the vocal cords are set into vibration ; consequently the pitch rises with increase of tension. The thyro-arytenoideus internus inserted into this anterior third of the vocal cord is thrown into vibration, together with the thin edge of the elastic ligament, where this band of muscle-fibres exists. We have therefore not only a short

string but a thin string vibrating and producing high-pitched notes varying according to the tension. Aikin, *ibid.*, says: "the glottic shock" cannot be accepted as a normal prelude to phonation. Aikin may be right for the human being, but obviously for the Gibbon this mechanism subserves a very useful purpose; for the "glottic shock" enables intercommunication at long distances. This valve also plays a very important part in fixation of the chest-walls necessary for the Gibbon's remarkable vigorous action of the arms.

Negus, Arris and Gale Lecture, "The Mechanism of the Larynx," states, "The free and undercut lower margins of the ary-epiglottic folds (*ride* fig. 1 B, fig. 2 A), in a form capable of functioning as a valve, are almost entirely limited to the anthropoid apes and Man." Sir Arthur Keith has shown that the mobility of the upper ribs is also peculiar to the anthropoids and Man, and this necessitates a special valve mechanism, so that when the diaphragm contracts forcibly and fills the lungs the air may be retained under increased pressure. When the chest is filled by deep inspiration the ribs are then spread out. The valve closing the glottis affords a fixed support for the powerful muscles having attachment to the ribs and upper limbs. When the animal therefore has to make a great effort with its arms, especially when they are adducted, the breath is prevented from escaping by this valve and the ribs from falling in. It is reasonable to assume that the great development of this valve was primarily connected then with the arboreal habits of the anthropoid apes. It might be asked, why does this valve not exist, upon this hypothesis, in primates generally? Possibly the answer is more perfect dissociation of the fore limbs together with weight and size, or very great agility as in the Gibbons. This valve then may be correlated in its primary function with closure of the glottis and fixation of the upper part of the chest in the anthropoid apes. But the Gibbon also employs it with great effect in the production of loud vocal sounds.

The power of variations in pitch, which the Gibbon possesses, may be a means of emotional intercommunication which the other anthropoids do not possess to the same degree.

Elliot Smith, 'Evolution of Man,' states: "While still in the Simian stage of development man's ancestors were already equipped with all the specialised muscles needed for articulate speech and the cerebral apparatus for controlling their movements and for acquiring skill to learn new methods of action." Thus the Gibbon, the most erect of the anthropoid apes, has a superior anatomical development for the production of musical vocal sounds to the Gorilla.

If the *Pithecanthropus erectus* of Dubois is on the same stem as the Gibbon, the existence of this vocal muscle in the Gibbon is of biological interest from an evolutionary point of view.

EXPLANATION OF PLATES II.-V.*

Fig. 1. Vertical section of larynx with a scale of millimetres. *S. S.*, squamous
epithelium ; *El.*, elastic tissue ; *Th.Ar.*, thyro-arytenoid muscle.
Th., thyroid cartilage ; *Gl.*, mucous glands ; *Cric.*, cricoid cartilage ;
Th.Cr., crico-thyroid muscle ; *Trach.*, trachea ; T. 25, T. 43, T. 55,
levels of horizontal sections.

Fig. 2, T. 25. *Sac.*, sacculus ; *El.*, band of elastic tissue in the aryteno-epiglottic
fold ; *Sant.*, cartilages of Santorini or cornicula ; *Ar.*, arytenoid carti-
lage.

Fig. 8, T. 43. *S.-S.*, squamous epithelium ; *Gl.*, mucous glands ; *Pr.voc.*, pro-
cessus vocalis of arytenoid cartilage ; *Ar.*, arytenoid cartilage ; *Cr.*,
cricoid cartilage ; *Th.Ar.*, thyro-arytenoid muscle ; *Lat.Cr.Ary.*, lateral
crico-arytenoid muscle ; *Thy.Cr.*, crico-thyroid muscle ; *St.Th.*, sterno-
thyroid muscle.

Figs. 4 & 5, T. 46 & 47. Same as Fig. 3, but posterior crico-arytenoid muscle post
Cr.Ar. seen.

Fig. 6, Areas 12 & 13, which show microscopic structure of the vocal muscle,
figs. 12 & 13.

Figs. 7, 8, 9, 10, 11, Sections T. 48-T. 55. Lettering indicating structures seen in
sections at lower levels, the same as above.

Fig. 12, Pl. V. Section of area 12, fig. 6. The termination of striped muscle-fibres
of the *Thy.Ar.* internus amidst the elastic fibres of the vocal cord.
Scale of measurement.

Fig. 13, Pl. I. Section of area 13, fig. 6, showing the rounded ends of muscle-fibres
surrounded by a cap of tendinous tissue, separating the thyro-aryte-
noideus internus, *Thy.Ar.*, from the thyro-arytenoideus.

* For explanation of Plate I., see pp. 1164-1165.

EXHIBITIONS AND NOTICES.

October 21st, 1924.

Sir ARTHUR SMITH WOODWARD, F.R.S., F.Z.S., Vice-President,
in the Chair.

The SECRETARY read the following Report on the Additions
to the Society's Menagerie during the months of May, June,
July, August, and September, 1924 : —

MAY.

The registered additions to the Society's Menagerie during
the month of May were 226 in number. Of these 95 were
acquired by presentation, 23 were deposited, 91 were purchased,
1 was received in exchange, and 16 were born in the Menagerie.

The following may be specially mentioned : —

6 Wanderoo Macaques (*Macacus silenus*), from Southern India,
purchased on May 2nd.

1 Red Tiger-Cat (*Felis aurata*), from Dahomey, presented by
Herbert H. Edis, Esq., on May 19th.

1 Dinemelli Weaver-bird (*Dinemellia dinemelli*), from Abyssinia,
new to the Collection, presented by G. B. Chapman, Esq., F.Z.S.,
on May 14th.

2 Great-billed Ravens (*Corvultur crassirostris*), from N.E. Africa,
deposited on May 24th.

2 Wagler's Conures (*Conurus wagleri*), from Colombia, presented
by W. K. Pomeroy, Esq., on May 27th.

2 Bouquet's Amazons (*Chrysotis bouqueti*), from Dominica,
purchased on May 14th.

4 Blackish Tortoises (*Testudo nigrita*), from the Galapagos
Islands, 2 purchased and 2 deposited on May 16th.

3 Gigantic Cyclagras (*Cyclagras gigas*), from South America,
new to the Collection, deposited on May 23rd.

JUNE.

The registered additions to the Society's Menagerie during
the month of June were 191 in number. Of these 57 were
acquired by presentation, 29 were deposited, 51 were purchased,
and 54 were born in the Menagerie.

The following may be specially mentioned : —

1 Black-faced Spider-Monkey (*Ateles ater*), presented by
Arthur A. Haserick, Esq., F.Z.S., on June 23rd.

1 Tiger-Lion hybrid ♂ bred at Nawanagar, India, and presented by Lt.-Col. H.H. The Maharajah Jam Sahib of Nawanagar, G.C.S.I., G.B.E., on June 21.

A collection of animals from Rio de Janeiro, presented by Sir Henry J. Lynch, F.Z.S., on June 19th, consisting of 3 Capybaras (*Hydrochœrus hydrochœrus*), 1 Spotted Cavy (*Cœlogenys paca*), 3 Hairy-rumped Agoutis (*Dasyprocta prymnolopha*), 1 Red Brocket (*Mazama rufa*), 1 Six-banded Armadillo (*Euphractus sexcinctus*), and 1 Violaceous Night-Heron (*Nyctanassa violaceus*).

2 Kangaroo-Island Kangaroos (*Macropus fuliginosus*), new to the Collection, purchased on June 19th.

JULY.

The registered additions to the Society's Menagerie during the month of July were 330 in number. Of these 269 were acquired by presentation, 19 were deposited, 13 were purchased, 3 were received in exchange, and 26 were born in the Menagerie.

The following may be specially mentioned:—

A collection, from Gambia, presented by H.E. Captain C. H. Armitage, C.M.G., D.S.O., F.Z.S., on July 14th, consisting of Harnessed and Nagor Antelopes, Porcupines, Mongooses, Duikers, Caracals and other mammals, Hooded Vultures, Marabou Storks and other birds, Monitors and other reptiles.

2 Gelada Baboons and 4 Pigmy Falcons, from Abyssinia, presented by Gilbert Blaine, F.Z.S., on July 18th.

1 Bel Pheasant, from Tonquin, and 1 Edwards's Pheasant, from Annam, new to the Collection, presented by Jean Delacour, F.Z.S., on July 9th.

AUGUST.

The registered additions to the Society's Menagerie during the month of August were 153 in number. Of these 55 were acquired by presentation, 14 were deposited, 55 were purchased, 15 were received in exchange, and 14 were born in the Menagerie.

The following may be specially mentioned:—

2 Chimpanzees (*Anthropopithecus troglodytes*), from West Africa, deposited on August 11th.

1 White-thighed Colobus (*Colobus vellerosus*), from West Africa, deposited on August 31st.

1 European Bison (*Bison bonarus*), from Central Europe, deposited on August 26th.

6 Argentine Flamingoes (*Phœnicopterus chilensis*), from South America, received in exchange on August 26th.

SEPTEMBER.

The registered additions to the Society's Menagerie during the month of September were 125 in number. Of these 73 were

acquired by presentation, 11 were deposited, 31 were purchased, and 10 were born in the Menagerie.

The following may be specially mentioned :—

1 Musk-Ox (*Ovibos moschatus*), from Greenland, purchased on September 15th.

1 Sudanese Oryx (*Oryx algazel*), from Nigeria, presented by The Emir of Katsina on September 16th.

1 Dromedary (*Camelus dromedarius*), presented by A. H. Wingfield, Esq., on September 17th.

2 Canadian Beavers (*Castor canadensis*), from Toronto, presented by the Special Service Squadron on September 30th.

2 " Blue " specimens of the Black Rat (*Rattus rattus*), presented by H. C. Brooke, Esq., on September 7th.

1 Imperial Parrot (*Amazona imperialis*), from Dominica, purchased on September 23rd.

1 Albino Indian Cobra (*Naia tripudians*), deposited on September 1st.

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The Hon. IVOR MONTAGU, F.Z.S., exhibited, and made remarks upon, some living Dormice from Wienerwalden, Vienna.

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Prof. H. M. LEFROY, M.A., F.Z.S., exhibited, and made remarks upon, a series of lantern slides illustrating the life-history and habits of the Death-Watch Beetle, and drew especial attention to the serious damage that is being caused by this insect in its larval stage to the oak beams in the roofs of ancient buildings throughout the country.

November 4th, 1924.

Prof. E. W. MACBRIDE, F.R.S., Vice-President,
in the Chair.

Sir ARTHUR SMITH WOODWARD, F.R.S., F.Z.S., exhibited, and made remarks upon, a plaster cast of a Fossil Egg of a Dinosaur.

———

Mr. D. SETH-SMITH, F.Z.S., exhibited a living specimen of the rare Amazon Parrot, *Amazona imperialis*, and a pair of the almost equally rare *Amazona bouqueti*, the two species of the genus inhabiting the island of Dominica in the Lesser Antilles. These parrots were apparently very uncommon in the island, and had rarely been imported alive to Europe.

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Mr. SETH-SMITH also exhibited the " bower " of the Australian Regent Bird, *Sericulus melinus*, which had been constructed in the " Summer Aviary " during the past summer.

Mr. E. G. BOULENGER, F.Z.S., exhibited, and made remarks upon (1) Hybrid Fish and cases of sex-invasion; (2) Abnormal male specimen of the " Millions" Fish (*Lebistes reticulatus*).

Mr. R. H. BURNE, F.Z.S., exhibited, and made remarks upon, specimens showing the use of *intra vitam* staining by madder in the study of bone-growth.

Last of the Passenger-Pigeons (Ectopistes migratorius).

The SECRETARY read the following note from Mr. HUGH S. GLADSTONE, M.A., F.Z.S., on the date of death of the last of the Passenger-Pigeons (*Ectopistes migratorius*):—

"In the ' Proceedings of the Zoological Society of London,' part ii. 1921, pp. 441-2, it is stated that the last of the Passenger-Pigeons (*Ectopistes migratorius*), a female, died in the Zoological Gardens of Cincinnati in September 1913, where she had lived in captivity for a number of years with others of the same species. From time to time these others died, until only the female remained—the sole living representative of the endless millions that originally were to be found in the United States.

"I have made enquiries, and find that (as stated in ' Portraits and Habits of our Birds, edited by T. Gilbert Pearson, vol. i. 1920, p. 22) the actual date was 1st September, 1914."

November 18th, 1924.

Sir ARTHUR SMITH WOODWARD, F.R.S., F.Z.S., Vice-President, in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the month of October, 1924:—

The registered additions to the Society's Menagerie during the month of October were 209 in number.. Of these 129 were acquired by presentation, 6 were deposited, 16 were purchased, 4 were received in exchange, and 54 were born in the Menagerie.

The following may be specially mentioned:—

1 Grant's Zebra (*Equus quagga granti*) ♂, 2 East African Elands (*Taurotragus oryx pattersonianus*) ♂ ♀, and 1 Buffalo (*Bos caffer*) ♀, from Kenya Colony, presented by Maj.-General Sir Edward Northey, G.C.M.G., C.B., F.Z.S., on October 6th.

1 Buffalo (*Bos caffer*) ♂, from Kenya Colony, presented by Capt. Keith Caldwell, R.A.F., F.Z.S., on October 6th.

1 Beisa Oryx (*Oryx beisa*) ♂, from Kenya Colony, presented by Miss Katherine Beynon on October 6th.

1 Polar Bear (*Thalarctos maritimus*) ♂, from Hudson Straits, presented by Capt. Thos. Smellie on October 24th.

2 Mallee Birds (*Lipoa ocellata*), from South Australia, deposited by H.M. The King on October 23rd.

1 White-backed Vulture (*Pseudogyps africanus*), 1 Bashful Tree-Frog (*Rappia concolor*), both new to the Collection, and a number of birds and reptiles, presented by H.E. Capt. C. H. Armitage, C.M.G., D.S.O., F.Z.S., on October 15th.

Mr. L. C. BUSHBY exhibited a collection of specimens from the Caird Insect House.

Mr. A. NIALL RANKIN, F.Z.S., exhibited, and made remarks upon, a series of photographs of Bird Life which he had taken during the Oxford Spitsbergen Expedition.

Vertebra of a Blue Whale.

Sir SIDNEY F. HARMER, K.B.E., Sc.D., V.P.R.S., F.Z.S., exhibited a vertebra of a Blue Whale from South Georgia. The specimen is the larger of two vertebræ recently presented to the British Museum (Natural History) by the Southern Whaling and Sealing Company, Ltd., after having been shown in the Falkland Islands section of the Wembley Exhibition. Both are apparently from the early lumbar region, and might have belonged to the same whale.

The vertebra exhibited is of large size, measuring 4 ft. 2 in. in total height. 5 ft. 0 in. across the transverse processes *, the centrum being 1 ft. 4 in. in dorsoventral diameter and 1 ft. 6⅞ in. and 1 ft. 7¾ in. in transverse diameter at the anterior and posterior ends respectively. The epiphyses had become detached and were not received.

The principal interest of the specimen is the evidence it supplies with regard to the size at which the epiphyses become ankylosed to the centra in the Southern Blue Whale. A similar vertebra, in which the epiphyses are fully ankylosed, was brought home by Mr. P. Stammwitz from South Georgia, at the conclusion of the Expedition 1913/14, undertaken by Major G. E. H. Barrett-Hamilton, who died soon after his arrival on the island. The vertebra was from a female Blue Whale 91 feet in length, as measured by Mr. Stammwitz. It is slightly larger, in its principal measurements, than the bone now exhibited, the total height being 4 ft. 8 in. and the width across the transverse processes 5 ft. 7⅓ in. This points to a length estimated as 83 to 84 feet for the whale to which the exhibited vertebra belonged. From its position in the series, it is possible that ankylosis of the epiphyses may already have commenced at the cervical and caudal ends of the vertebral column (see note on

* The right transverse process seems to be abnormally short (R., 1 ft. 4 in.; L., 2 ft. 0 in.).

Flower's results, Proc. Zool. Soc. 1923, p. 1087). A conclusion which can be drawn from these specimens is that, in a Blue Whale of presumably 83 to 84 feet in length, the ankylosis of the epiphyses is unfinished, while in a larger specimen, 91 feet in length, of the same species and from the same locality, it is complete, and the specimen is fully adult. On the analogy of facts known to human anatomists growth should cease at this stage : and it would appear to follow that the small proportion of Blue Whales which have been recorded as reaching a greater length, even up to 100 feet or slightly more, are specially large individuals, in which the ankylosis of the epiphyses might be expected to have commenced and terminated at body-lengths greater than those here recorded. This would imply a variability in body-length of at least 10 feet, but it is not improbable that a certain proportion of Southern Blue Whales will be found to reach their full size without reaching a length of 80 feet.

The question has still to be decided whether the Southern Blue Whale is specifically identical with its Northern representative. Lönnberg (K. Svensk. Vet.-Akad. Handl. 1906, vol. xl. No. 5, p. 27) has expressed the opinion that it is desirable to regard them as distinct, at least until their identity has been proved; and he refers the Southern form to *Balænoptera intermedia* Burm. In this connection it may be pointed out that the neural spines of the two Southern individuals under consideration are distinctly longer and narrower, relatively, than those of the Wexford Blue Whale (*B. musculus*) referred to by me in the note above quoted.

Mr. E. G. BOULENGER, F.Z.S., exhibited, and made remarks upon, some fish (*Cyprinodon dispar*) caught by Major R. E. Cheesman, C.M.Z.S., in the hot springs in the Hufuf Oasis of Arabia, in water at a temperature of between 101° and 106° Fahr.

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Dr. G. M. VEVERS, F.Z.S., exhibited, and made remarks upon, a Leopard's Skin, showing abnormal coloration due to injury.

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[New names in clarendon type. Systematic references in italics.
(z. s. l.) indicates additions to the Society's Menagerie.]

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

May 6th, 1924.

Prof. E. W. MacBride, F.R.S., Vice-President,
in the Chair.

Dr. G. M. Vevers, F.Z.S., exhibited, and made remarks upon, a Leech (*Placobdella* sp.) from the American Terrapin *Chrysemys floridana*.

Mr. R. I. Pocock, F.R.S., F.Z.S., exhibited, and made remarks upon, a photograph of a Seal.

Prof. J. P. Hill, F.R.S., F.Z.S., exhibited, and made remarks upon, the Fœtus of a Fin-Whale.

Mr. D. Seth-Smith, F.Z.S., exhibited, and made remarks upon, two female Pheasants assuming male plumage.

Prof. D. M. S. Watson, F.R.S., F.Z.S., gave a *résumé* of Dr. R. Broom's paper "On some Points in the Structure of the Pareiasaurian Skull."

Prof. D. M. S. WATSON, F.R.S., F.Z.S., communicated his paper on " The Elasmosaurid Shoulder-Girdle and Fore-Limb."

The next Meeting of the Society for Scientific Business will be held on Tuesday, May 20th, at **5.30 P.M.**, when the following Communications will be made :—

THE SECRETARY.

Report on the Additions to the Society's Menagerie during the month of April, 1924.

Major S. S. FLOWER, O.B.E., F.Z.S.

Exhibition of a remarkable Tortoise of the genus *Testudo*.

Sir SIDNEY F. HARMER, K.B.E., Sc.D., V.P.R.S., F.Z.S.

On *Mesoplodon* and other Beaked Whales.

R. I. POCOCK, F.R.S., F.Z.S.

Some External Characters of *Orycteropus afer*.

The following Papers have been received :—

HELGA S. PEARSON.

(1) The Skull of the Dicynodont Reptile *Kannemeyeria*.
(2) A Dicynodont Reptile reconstructed.

R. I. POCOCK, F.R.S., F.Z.S.

The External Characters of the Pangolins (Manidæ).

MARY L. HETT, B.Sc., F.R.S.

On a new Land-Nemertean from New South Wales.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

Secretary.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
May 13th, 1924.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

May 20th, 1924.

Dr. A. Smith Woodward, F.R S., Vice-President,
in the Chair.

The Secretary read a Report on the Additions to the Society's Menagerie during the month of April, 1924.

Major S. S. Flower, O.B.E., F.Z.S., exhibited, and made remarks upon, a remarkable Tortoise of the genus *Testudo*.

Mr. F. Martin Duncan, F.Z.S., exhibited, and made remarks upon, the skin and hair of a Platypus (*Ornithorhynchus anatinus*) from Tasmania.

Miss E. M. Knobel, F.Z.S., exhibited, and made remarks upon, the Pelvic Bones of the Blue-fronted Amazon and other Parrots.

Sir Sidney F. Harmer, K.B.E., Sc.D., V.P.R.S., F.Z.S., exhibited, and made remarks upon, a specimen of Ambergris taken from the intestine of a Sperm-Whale in the Straits of Gibraltar.

Sir Sidney F. Harmer, K.B.E., Sc.D., V.P.R.S., F.Z.S., gave a *résumé* of his paper "On *Mesoplodon* and other Beaked Whales."

Mr. R. I. Pocock, F.R.S., F.Z.S., communicated his paper on "Some External Characters of *Orycteropus afer*.'

The next Meeting of the Society for Scientific Business will be held on Tuesday, June 3rd, 1924, at **5.30** P.M., when the following communications will be made :—

HELGA S. PEARSON.

(1) The Skull of the Dicynodont Reptile *Kannemeyeri*.

(2) A Dicynodont Reptile reconstructed.

R. I. POCOCK, F.R.S., F.Z.S.

The External Characters of the Pangolins (Manidæ).

Prof. J. P. HILL, F.R.S., F.Z.S., and E. A. FRASER, M.D.

Some Observations on the Female Urogenital Organs of the Didelphyidæ.

MARY L. HETT, B.Sc., F.Z.S.

On a new Land-Nemertean from New South Wales.

HEM SINGH PRUTHI, M.Sc.

(1) On the Post-Embryonic Development and Homology of the Male Genital Organs of *Tenebrio molitor* (Coleoptera).

(2) On the Development of the Ovipositor and the Efferent Genital Ducts in *Tenebrio molitor* (Coleoptera), with Remarks on the Comparison of the latter Organs in the two Sexes.

CHARLES F. SONNTAG, M.D., F.Z.S.

(1) The Comparative Anatomy of the Tongues of the Mammalia.—X. Rodentia.

(2) The Comparative Anatomy of the Tongues of the Mammalia.—XI. Marsupialia and Monotremata.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed, and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

Secretary.

Zoological Society of London,
 Regent's Park, London, N.W. 8.
 May 27th, 1924.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

June 3rd, 1924.

Prof. E. W. MacBride, F.R.S., F.Z.S., Vice-President,
in the Chair.

Mr. D. Seth-Smith, F.Z.S., exhibited, and made remarks upon, a photograph of Elephant twins.

Miss Helga S. Pearson communicated her papers on (1) "The Skull of the Dicynodont Reptile *Kannemeyeri*"; and (2) "A Dicynodont Reptile reconstructed.

Mr. R. I. Pocock, F.R.S., F.Z.S., communicated his paper on " The External Characters of the Pangolins (Manidæ)."

A *résumé* of the paper by Prof. J. P. Hill, F.R.S.. F.Z.S., and E. A. Fraser, M.D., F.Z.S., on "Some Observations on the Female Urogenital Organs of the Didelphyidæ," was communicated by Dr. Fraser.

In the absence of the Authors the following papers were taken as read:—MARY L. HETT, B.Sc., F.Z.S., "On a new Land-Nemertean from New South Wales." HEM SINGH PRUTHI, M.Sc.: (1) " On the Post-Embryonic Development and Homology of the Male Genital Organs of *Tenebrio molitor* (Coleoptera) "; (2) "On the Development of the Ovipositor and the Efferent Genital Ducts in *Tenebrio molitor* (Coleoptera), with Remarks on the Comparison of the latter Organs in the two Sexes." CHARLES F. SONNTAG, M.D., F.Z.S.: (1) " The Comparative Anatomy of the Tongues of the Mammalia.—X. Rodentia "; (2) " The Comparative Anatomy of the Tongues of the Mammalia.—XI. Marsupialia and Monotremata."

The next Meeting of the Society for Scientific Business will be held on Tuesday, October 21st, 1924, at **5.30** P.M.

A notice stating the Agenda for the Meeting will be circulated early in October.

The following Papers have been received :—

R. I. POCOCK, F.R.S., F.Z.S.

On the External Characters of the South American Edentates.

EKENDRANATH GHOSH, M.Sc., M.D., F.Z.S., F.R.M.S.

On the Anatomy of *Parallepipedum* Linné (Mollusca).

Rev. F. J. WYETH, D.Sc., M.A., B.D., F.Z.S.

The Development and Neuromery of the Fore-brain in *Sphenodon*.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed and be limited so far as possible to the description of new results.

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P. CHALMERS MITCHELL,

Secretary.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
June 10th, 1924.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

October 21st, 1924.

Sir Arthur Smith Woodward, F.R.S., F.Z.S.,
Vice-President, in the Chair.

The Secretary read a Report on the Additions to the Society's Menagerie during the months of June, July, August, and September, 1924.

The Hon. Ivor Montagu, F.Z.S., exhibited, and made remarks upon, some living Dormice from Wienerwalden, Vienna.

Prof. H. M. Lefroy, M.A., F.Z.S., exhibited, and made remarks upon, a series of lantern-slides illustrating the life-history and habits of the Death-Watch Beetle, and drew especial attention to the serious damage that is being caused by this insect in its larval stage to the oak beams in the roofs of ancient buildings throughout the country.

Miss Joan B. Procter, F.L.S., F.Z.S., Curator of Reptiles, communicated her paper on "Unrecorded Characters seen in Living Snakes and Description of a new Tree-Frog."

The Rev. F. J. WYETH, M.C., D.Sc., M.A., B.D., F.Z.S., gave a *résumé* of his paper on " The Development and Neuromery of the Fore-brain in *Sphenodon*."

Mr. R. I. POCOCK, F.R.S., F.Z.S., communicated his paper " On the External Characters of the South American Edentates."

In the absence of the Author, Mr. H. C. ABRAHAM'S paper on " Some Mygalomorph Spiders from the Malay Peninsula " was taken as read.

The next Meeting of the Society for Scientific Business will be held on Tuesday, November 4th, at 5.30 P.M., when the following Communications will be made :—

Sir A. SMITH WOODWARD, F.R.S., F.Z.S.

Exhibition of a plaster cast of a Fossil Egg of a Dinosaur.

D. SETH-SMITH, F.Z.S.

Exhibition of Rare Amazon Parrots from Dominica and bower of Australian Regent-Bird.

STANLEY HIRST, F.Z.S.

Three new Acari belonging to the Superfamily Trombidioidea (Erythræidæ and Teneriffiolidæ).

IVOR MONTAGU, F.Z.S.

(1) On the Remains of Fen-Beaver in the Sedgwick Museum; (2) On the Burrows of the Rodent *Spalax*.

ROBERT GURNEY, M.A., F.Z.S.

The Larval Development of some British Prawns (Palæmonidæ).—II. *Leander longirostris* and *Leander squilla*.

W. E. LE GROS CLARK, F.R.C.S.Eng., F.Z.S.

    On the Brain of the Tree-Shrew *Tupaia minor.*

The following Papers have been received :—

MAURICE BURTON, M.Sc.

    A Revision of the Sponge Family Donatidæ.

DORIS R. CROFTS, M.Sc., F.Z.S.

    The Comparative Morphology of the Cæcal Gland (Rectal Gland) of Selachian Fishes.

C. R. NARAZANA RAO, M.A., and M. S. MEHKRI, B.Sc.

    A Case of Budding in *Megascolex* (*Lampito*) *mauritii* Kinb.

ISABELLA GORDON, B.Sc.

    Gorgonacea from the Indian Ocean.

S. MAULIK, F.Z.S, and C. DOVER, F.E.S.

    The Larva and Pupa of an Indian Cassid Beetle (*Prioptera decemmaculata* Boh.).

H. E. ANDREWES, F.Z.S.

    A Revision of the Oriental Species and Genus *Tachys* (Coleoptera).

EKENDRA NATH GHOSH, M.Sc., M.D., F.Z.S.

    On the Anatomy of *Parallepipedum* Klein. (Mollusca).

PERCY R. LOWE, B.A., M.B., F.Z.S.

    On the Anatomy and Systematic Position of the Madagascan Bird *Mesites.*

Sir FREDERICK MOTT, K.B.E., F.R.S.

    Notes on the Gibbon Larynx made during Dissection.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. Papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

Secretary.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
October 28*th*, 1924.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

November 4th, 1924.

Prof. E. W. MacBride, F.R.S., Vice-President,
in the Chair.

Sir Arthur Smith Woodward, F.R.S., F.Z.S., exhibited, and made remarks upon, a plaster cast of a Fossil Egg of a Dinosaur.

Mr. D. Seth-Smith, F.Z.S., exhibited, and made remarks upon, some rare Amazon Parrots from Dominica and a bower of the Australian Regent-Bird.

Mr. E. G. Boulenger, F.Z.S., exhibited, and made remarks upon, (1) Hybrid Fish and cases of sex-inversion; (2) abnormal male specimens of the " Millions Fish " *Tebistes reticulatis.*

Mr. R. H. Burne, M.A., F.Z.S., exhibited, and made remarks upon, specimens showing the use of *intra vitam* staining by madder in the study of bone-growth.

The Secretary read the following note from Mr. Hugh S. Gladstone, M.A., F.Z.S., on the date of death of the last of the Passenger-Pigeons (*Ectopistes migratorius*):—

" In the ' Proceedings of the Zoological Society of London,' part ii. 1921, pp. 441-2, it is stated that the last of the

Passenger-Pigeons (*Ectopistes migratorius*), a female, died in the Zoological Gardens of Cincinnati in September 1913, where she had lived in captivity for a number of years with others of the same species. From time to time these others died, until only the female remained—the sole living representative of the endless millions that originally were to be found in the United States.

"I have made enquiries, and find that (as stated in ' Portraits and Habits of our Birds,' edited by T. Gilbert Pearson, vol. i. 1920, p. 22) the actual date was 1st September, 1914."

Mr. STANLEY HIRST, F.Z.S., gave a *résumé* of his paper "Three new Acari belonging to the Superfamily Trombidioidea (Eiythræidæ and Teneriffiolidæ)."

Mr. IVOR MONTAGU, F.Z.S., communicated his papers (1) "On the Remains of Fen-Beaver in the Sedgwick Museum" and (2) "On the Burrows of the Rodent *Spalax*."

In the absence of the Author, Mr. ROBERT GURNEY's paper on "The Larval Development of some British Prawns (Palæmonidæ).—II. *Leander longirostris* and *Leander squilla*," was taken as read.

Mr. W. E. LE GROS CLARK, F.R.C S.Eng., F.Z.S., communicated his paper on "The Brain of the Tree-Shrew, *Tupaia minor*."

The next Meeting of the Society for Scientific Business will be held on Tuesday, November 18th, 1924, at 5.30 P.M., when the following Communications will be made:—

THE SECRETARY.

Report on the Additions to the Society's Menagerie during the month of October 1924.

L. C. BUSHBY.

Exhibition of specimens from the Caird Insect House.

A. NIALL RANKIN, F.Z.S.

Exhibition of photographs taken during the Oxford Spitsbergen Expedition.

MAURICE BURTON, M.Sc.

A Revision of the Sponge Family Donatidæ.

PERCY R. LOWE, B.A., M.B., F.Z S.

On the Anatomy and Systematic Position of the Madagascan Bird *Mesites*.

Sir FREDERICK MOTT, K.B.E., F.R.S.

Notes on the Gibbon Larynx made during Dissection.

EKENDRA NATH GOSH, M.Sc., M.D., F.Z.S.

On the Anatomy of *Parallepipedum* Klein (Mollusca).

The following Papers have been received :—

DORIS R. CROFTS, M.Sc., F.Z.S.

The Comparative Morphology of the Cæcal Gland (Rectal Gland) of Selachian Fishes.

S. MAULIK, F.Z.S., and C. DOVER, F.E.S.

The Larva and Pupa of an Indian Cassid Beetle (*Prioptera decemmaculata* Boh.).

STANLEY HIRST, F.Z.S.

Descriptions of New Acari, mainly parasitic on Rodents.

Prof. O. FUHRMANN, Ph.D., and JEAN G. BAER, D.Sc.

Zoological Results of the Third Tanganyika Expedition conducted by Dr. W. A. Cunnington, F.Z.S., 1904–1905.—Report on the Cestoda.

ARTHUR LOVERIDGE, C.M Z.S., F.E S.

On *Natrix olivacea* Peters (Reptilia), from Pemba Island, and other Notes.

R. I. POCOCK, F.R.S., F.Z.S.

The External Characters of an American Badger (*Taxidea taxus*) and an American Mink (*Mustela vison*) recently exhibited in the Society's Gardens.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed, and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

Secretary.

ZOOLOGICAL SOCIETY OF LONDON,
   REGENT'S PARK, LONDON, N.W. 8.
      November 11th, 1924.

No. 258.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

November 18th, 1924.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,
in the Chair.

The SECRETARY read a Report on the Additions to the Society's Menagerie during the month of October, 1924.

Mr. L. C. BUSHBY exhibited a collection of specimens from the Caird Insect House.

Mr. A. NIALL RANKIN, F.Z.S., exhibited, and made remarks upon, a series of photographs of bird-life which he had taken during the Oxford Spitsbergen Expedition.

Sir SIDNEY F. HARMER, K.B.E., V.P.R.S., F.Z.S., exhibited, and made remarks upon, a Vertebra of the Southern Blue Whale.

Mr. E. G. BOULENGER, F.Z.S., Director of the Aquarium, exhibited some fish (*Cyprinodon dispar*) caught by Major R. E. Cheesman, C.M.Z.S., in the hot springs in the Hufuf Oasis of Arabia in water at a temperature of between 101° and 106° F.

Dr. G. M. VEVERS, F.Z.S., exhibited, and made remarks upon, a Leopard's Skin showing abnormal coloration.

Sir FREDERICK MOTT, K.B.E., F.R.S., gave a *résumé* of his paper "Notes on the Gibbon Larynx made during Dissection."

Mr. PERCY R. LOWE, B.A., M.B., F.Z.S., communicated his paper "On the Anatomy and Systematic Position of the Madagascan Bird *Mesites*."

Owing to the lateness of the hour, the following communications were taken as read :—S. MAULIK, F.Z.S., and C. DOVER, F.E.S., "The Larva and Pupa of an Indian Cassid Beetle (*Prioptera decemmaculata* Boh.)"; MAURICE BURTON, M.Sc., "A Revision of the Sponge Family Donatiidæ"; EKENDRA NATH GOSH, M.Sc., M.D., F.Z.S., "On the Anatomy of *Parallepipedum* Klein (Mollusca)."

The next Meeting of the Society for Scientific Business will be held on Tuesday, February 3rd, at 5.30 P.M.

A Notice stating the Agenda for the Meeting will be circulated early in January.

The following Papers have been received :—

DORIS R. CROFTS, M.Sc., F.Z.S.

The Comparative Morphology of the Cæcal Gland (Rectal Gland) of Selachian Fishes.

STANLEY HIRST, F.Z.S.

Descriptions of New Acari, mainly parasitic on Rodents.

Prof. O. FUHRMANN, Ph.D., and JEAN G. BAER, D.Sc.

Zoological Results of the Third Tanganyika Expedition conducted by Dr. W. A. Cunnington, F.Z.S., 1904-1905.—Report on the Cestoda.

ARTHUR LOVERIDGE, C.M.Z.S., F.E.S.

On *Natrix olivacea* Peters (Reptilia), from Pemba Island, and other Notes.

R. I. POCOCK, F.R S., F.Z.S.

The External Characters of an American Badger (*Taxidea-taxus*) and an American Mink (*Mustela vison*) recently exhibited in the Society's Gardens.

EDWARD PHELPS ALLIS, Jun., F.L.S., F.Z.S.

On the Origin of the V-shaped Branchial Arch in the Teleostomi.

R. I. POCOCK, F.R.S., F.Z.S.

Additional Notes on the External Characters of some Platy-rhine Monkeys.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,

Secretary.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
November 25th, 1924.

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